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A revision of the genera *Trachelostyla* and *Gonostomum* (Ciliophora, Hypotrichida), including redescriptions of *T. pediculiformis* (Cohn, 1866) Kahl, 1932 and *T. caudata* Kahl, 1932

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Introduction

Hypotrich ciliates are commonly encountered in many and diverse habitats. As Corliss (1979) noted, the taxonomy of this group is still confused, indeed some species, genera and even families are awaiting assignment to their proper taxonomic positions. When one genus of hypotrich, *Trachelostyla,* was isolated from marine interstitial sediments during a previous study of the ciliate fauna of the southern coast of England (Carey & Maeda, 1985), some difficulty was encountered in understanding the taxonomic position of this organism and also the closely related genus *Gonostomum.* Recent revisions of these two genera by Borror (1972) and Buitkamp (1977) have not clarified their position, they have merely confused the taxonomy of the family Holostichidae by either synonymizing conspicuously different organisms in a single genus or by assigning many disimilar species to one taxon. Since *Trachelostyla* and *Gonostomum* have been isolated frequently from marine and terrestrial environments (Kahl, 1932; Gellért, 1956), a detailed taxonomic investigation of these two genera should provide useful information for future ecological studies. This work is intended to clarify the confusion between *Trachelostyla* and *Gonostomum*, and by virtue of a complete revision, provide a key to species of these two genera. Additionally the morphological features of *Trachelostyla pediculiformis* (Cohn, 1866) Kahl, 1932 and *T. caudata* Kahl, 1932 are redescribed.

Materials and methods

The hypotrich ciliates were collected from interstitial sediments at East Head, West Wittering, National Grid reference SZ7799, a short headland at Chichester Harbour where, in a previous study, six sampling stations had been established (Carey and Maeda, 1985). Stations 1 and 2 faced the English Channel and were exposed to rather intensive wave action, whereas calmer water prevailed at Stations 4, 5 and 6 at the northern-most extremity of the headland. On the eastern shoreline around Station 6 an extensive saltmarsh was present. Earlier results of sand analysis had indicated that the mean grain size of sand in this area varied between 170 μm and 250 μm. The 'detrital material' or content of particles less than 62 μm increased continuously from Station 1 to Station 6. This component was measured as approximately 100 times higher at Stations 5 and 5 than that at Stations 1 and 2. In October 1982 *Trachelostyla pediculiformis* was found at all the Stations except Station 1 whereas *Trachelostyla caudata* was isolated from fine sands with low content of detrital material, i.e. Stations 1, 2 and 3. Water temperature of the sediment was recorded as 14°C.

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In July 1983, the water temperature was 24°C and decaying macroalgae were observed in seawater overlying the sampling area. On this occasion *T. pediculiformis* was found at all Stations sampled (Stations 1, 2 and 3) while *T. caudata* was encountered only at Station 1.

The ciliates were extracted from sediment cores as soon as possible after sampling, by the seawater-ice method of Uhlig (1968). For the sediment sample collected in July 1983, water at low temperature (12°C) was used for extraction instead of crushed ice as the temperature drop killed too many organisms (Hartwig *et al.*, 1977). Samples from each Station were retained in seawater under constant aeration for further investigation. Some difficulty in handling the organisms was experienced due to their thigmotactic nature and inate fragility. Rapid transfer using a wide bore micropipette from extraction dish to glass slide overcame this problem. The ciliates were observed using Nomarski interference, phase contrast and brightfield illumination, and recorded on video tape for repeated observation. High resolution optics and video recording enabled observations to be made on living cells without recourse to silver staining techniques.

Nomenclature

Fauré-Fremiet (1961) proposed the new family Holostichidae in the suborder Stichotrichina to include those organisms which possess a row of right and left marginal cirri, an elongated body and macronuclei two to many in number, with differentiated frontal and transverse cirri in most cases. These characteristics are certainly found in the genera *Gonostomum* and *Trachelostyla* although Corliss (1979) suggested the transfer of these two genera to the family Oxytrichidae in the suborder Sporadotrichina, because some members of these taxa have distinctive marginal cirri and well developed frontoventral and transverse cirri.

The genus *Gonostomum* was proposed by Sterki (1878) who transferred *Oxytricha affinis* Stein, 1859 to *Gonostomum affine* because of the location and shape of the peristome area and the arrangement of frontoventral cirri. He also proposed that *Oxytricha strenua* Engelmann, 1862 be changed to *Gonostomum strenua.* Since then, these two species have been placed into several genera. Kent (1881–1882) pointed out that the name of *Gonostomum* closely resembled those of *Gonostoma* and *Gonostomus*, names already employed to designate certain genera of fish and molluscs. Consequently he proposed the new genus *Plagiotricha*, with *P. affinis* and *P. strenua.* The first detailed revision of this group was presented by Gourret and Roeser (1888), which is illustrated in Table 1. These authors did

Table 1 Revision of the genus *Stichochaeta* by Gourret & Roeser, 1888

Genus *Stichochaeta* Clap. & Lachm.
Syn. *Gonostomum* Sterki
Plagiotricha Sav. Kent
1. *Stichochaeta pediculiformis* Cohn
Syn. *Gonostomum pediculiforme* Maupas
2. *Stichochaeta affinis* (Stein)
Syn. *Oxytricha affinis* Stein
Gonostomum affine Sterki
Plagiotricha (*Gonostomum*) *affinis* Sav. Kent
3. *Stichochaeta strenua* (Englemann)
Syn.*Oxytricha strenua* Englemann
Plagiotricha strenua Sav. Kent
Gonostomum strenua Maupas
4. *Stichochaeta corsica* n. sp.
Stichochaeta corsica n. sp.

not accept the names *Gonostomum* or *Plagiotricha* and placed the two species mentioned above into the genus *Stichochaeta* as *S. affinis* and *S. strenua.* In their revision, which already contained *Stichochaeta pediculiformis* described by Cohn, 1866, they also described a new species *Stichochaeta corsica.* Maupas (1883) decided to transfer *S. pediculiformis* to the genus *Gonostomum* noting that a typical member of this genus *Stichochaeta cornuta* possessed quite different features in the peristome area and also cirral arrangements from that of *Gonostomum.* In 1929 Shibuya found and described a new species which he named *Gonostomum andoi.* Kahl in 1928 described *G. pediculiforme*, but in 1932, in contrast to the description of Maupas (1883), mentioned that certain details were sufficient to erect a new genus, *Trachelostyla.* He pointed out that the three filose cirri in the caudal area which Maupas (1883) described as caudal cirri were in fact dorsal cirri which can be seen from the ventral side. The discontinuity of the two marginal cirral rows in the posterior area is a characteristic feature of Kahl's description of *Trachelostyla.* Kahl (1932) placed two species in this genus, *T. pediculiformis* and a new marine species *T. caudata.* After the genus *Trachelostyla* was proposed, the nomenclature of this group became simplified in that only the genera *Gonostomum* and *Trachelostyla* were recognized by subsequent authors. *T. dubia* was described from marine interstitial sediments by Dragesco (1954). In publications dealing with the ciliated fauna in soils underlying moss and leaves, Gellért (1942, 1956, 1957) described 5 species which were attributed to the genus *Gonostomum, G. algicola, G. spirotrichoides, G. bryonicolum, G. ciliophorum* and *G. geleii.* The second major revision of this group was presented by Borror (1972) which unfortunately was given without detailed explanations (Table 2). He transferred the 4 species of *Gonostomum* described by Gellért (1956, 1957) to the genus *Trachelostyla* along with a species of *Urosoma* and a species of the genus *Stichotricha. T. pediculiformis* was retained as Kahl (1932) proposed. A major divergence from the established taxonomy was proposed in the removal of *Oxytricha affinis; Gonostomum affine* of Sterki, 1878 and its synonyms, to the genus *Gastrostyla. Trachelostyla dubia* Dragesco (1954) was also transferred by Borror (1972) to the genus *Gastrostyla. Gonostomum*

Table 2 Revision of the genera *Gonostomum* and *Trachelostyla* by Borror, 1972

Genus *Gonostomum* Sterki, 1878
1. *G. strenum* (Englemann, 1862) Sterki, 1978
   Syn. *Oxytricha strenuum* Englemann, 1862
      Oxytricha tricornis Milne, 1886

Genus *Trachelostyla* Kahl, 1932
1. *T. pediculiformis* (Cohn, 1866) Kahl, 1932
   Syn. Stichochaeta pediculiformis Cohn, 1866
      S. corsica Gourret & Roeser, 1887
      Gonostomum pediculiforme Maupas, 1883
2. *T. bryonicolum* (Gellért, 1956) n. comb.
   Syn. Gonostomum bryonicolum Gellért, 1956
3. *T. caudata* Kahl. 1932
4. *T. ciliophorum* (Gellért, 1956) n. comb.
   Syn. *Gonostomum ciliophorum* Gellért, 1956
5. *T. geleii* (Gellért, 1957) n. comb.
   Syn. *Gonostomum geleii* Gellért, 1957
6. *T. macrostoma* (Gellért, 1957) n. comb.
   Syn. *Urosoma macrostoma* Gellért, 1957
7. *T. simplex* (Kahl, 1932) n. comb.
   Syn. *Stichotricha simplex* Kahl, 1932
8. *T. spirotrichoides* (Gellért, 1956) n. comb.
   Syn. *Gonostomum spirotrichoides* Gellért, 1956

Table 3 Revision of the genus *Trachelostyla* by Buitkamp, 1977

Genus *Trachelostyla*
1. *Trachelostyla pediculiformis* (Cohn, 1866) Kahl, 1932
   Synonym: *Stichochaeta pediculiformis* Cohn, 1866
   Gonostomum pediculiforme Maupas, 1883
   S. corsica Gourret & Roeser, 1887
2. *Trachelostyla caudata,* Kahl, 1932
3. *Trachelostyla affine* (Stein, 1859) n. comb.
   Synonym: *Oxytricha affine* Stein, 1859
   Gonostomum andoi Shibuya, 1929
   G. affine (Stein, 1859) Kahl, 1932
   G. bryonicolum Gellért, 1956
   G. ciliophorum Gellért, 1956
   G. spirotrichoides Gellért, 1956
   G. geleii Gellért, 1957
   Gastrostyla affine (Stein, 1859) Borror, 1972
   Trachelostyla bryonicolum (Gellért, 1956) Borror, 1972
   T. ciliophorum (Gellért, 1956) Borror, 1972
   T. spirotrichoides (Gellért, 1956) Borror, 1972
   T. geleii (Gellért, 1957) Borror, 1972
   T. canadensis Buitkamp & Wilbert, 1974

strenua, and its synonyms including *Oxytricha tricornis* Milne (1886–1887) was the only species of this genus to be retained. A new species of *Trachelostyla, T. canadensis* was described by Buitkamp & Wilbert (1974) from prairie soil in Canada and three years later the last major revision of this group was undertaken by Buitkamp (1977), see Table 3. In the latter revision which was devoid of detailed explanatory information, both *Trachelostyla pediculiformis* and *T. caudata* were retained, but an unusual step was taken in the establishment of *Trachelostyla affine* n. comb. and the inclusion of seven species in *T. affine* under various synonyms. It should be noted that this new taxon contained a variety of morphological forms which, when carefully investigated, should not have been synonymized. The last species to have been described in the genus *Gonostomum* was *G. franzi* (1982) from Austrian soils.

As a result of these earlier revisions there are still species which have a dubious position in these genera. These include *Stichochaeta mereschkoviskii* Andrusov, 1886 which Kahl (1932) put forward as a possible *Trachelostyla,* and *Trachelostyla rostrata* of Lepși (1964) which is poorly described. A species of *Gonostomum, G. parvum* was found and described by Lepși according to Stiller (1977). However detailed information is not yet available for this species. The diagram of *Gonostomum franzi* given by Foissner (1982) clearly shows the presence of ventral cirral rows extending almost the full length of the body, and should not be included in the genus *Gonostomum. Gonostomum geleii* described by Gellért (1957) possesses certain characters that suggest its inclusion in the genus *Gonostomum,* however the shape of the body and transverse cirri indicate that this organism should be placed in another genus, probably *Urosoma.* Similarly Borror's (1972) decision to include *Urosoma macrostoma* and *Stichotricha simplex* was clearly based on a superficial resemblance of these organisms to *Trachelostyla.* However the decision to transfer *T. dubia* of Dragesco (1954) to the genus *Gastrostyla* in our opinion was correct. A detailed study of these organisms indicates that they should all be excluded from the genus *Gonostomum.* Jankowski (1979) proposed a new scheme of classification for the order Hypotrichida, including the transference of the genus *Trachelostyla* to the new subfamily Oxytrichinae. But as detailed information on these revisions were not given, the Jankowskian scheme of classification was not followed in the present work.

Although 3 major revisions have been undertaken on this group, little information has been given by authors in support of major taxonomic changes. Certainly with the confusion regarding these genera it is clearly essential that a complete and accurate revision should be undertaken.

Diagnosis of the Genus *TRACHELOSTYLA* Kahl, 1932

Gonostomum Maupas, 1883 *pro parte*
Stichochaeta Gourret & Roeser, 1888 *pro parte*

A free swimming genus of hypotrich with a fragile and elastic, but non-contractile body, 130–190 µm in length. This organism possesses a narrow neck-like constriction in the anterior region. The peristome area is confined to the left lateral border, its posterior part bending abruptly and extending nearly to the centre of the body. Five to 10 frontoventral cirri are present in the anterior region, but frontoventral cirri in the mid- and posterioventral area are absent. Five or six transverse cirri are distinct in the posterior and form an oblique row. There are two marginal cirral rows which are not confluent posteriorly. No caudal cirri are present. Fine dorsal cirri can be observed from the ventral side. These appear to make two rows at the edge of the body and where these terminate at the posterior end some authors in earlier descriptions have clearly misinterpreted these as caudal cirri. Numerous macronuclei are dispersed throughout the body. This genus is found in marine habitats, and may be described as truely interstitial.

Key to species of *Trachelostyla*

Posterior region rounded, membranelles of AZM thickened and distinctive	*pediculiformis*
Posterior region narrowed, membranelles of AZM fine and of uniform length	*caudata*

Trachelostyla pediculiformis (Cohn, 1866) Kahl, 1932

Stichochaeta pediculiformis Cohn, 1866
Gonostomum pediculiforme Maupas, 1883
Stichochaeta corsica Gourret & Roeser, 1888

MORPHOLOGICAL DESCRIPTION: This species was found in interstitial sediments at East Head, Chichester Harbour, England, during a taxonomic and ecological survey of marine interstitial ciliates, in October, 1982 and July, 1983 (Carey & Maeda, 1985). Water temperatures of the sediment were 14°C and 24°C, respectively. This highly psammophilic species has been commonly encountered in many coastal areas of Europe, Russia, North and South America and the Sea of Japan. The body is characteristically flexible. Its locomotion as well as its body shape is distinct enough to distinguish it from other ciliates, frequently moving forward and backward and repeatedly raising the 'head' region above the substrate, constantly searching between the sand grains.

The body is elongate, 136–196 µm in length (Fig. 1). The anterior region, which comprises one-third of entire body length, is attenuated and produced as a narrower neck-like process. The posterior end is rounded in this species. The peristome area is confined to the left lateral border of the anterior region for most of its length. The posterior quarter of peristome area is bent inwards, and eventually extends to near the centre of the body. The buccal opening is situated at the 'shoulder-like' ridge at the base of the 'neck' region. There are five long membranelles of the AZM at the anterior extremity. A bundle of several long cilia-like membranelles are clearly seen in the buccal area which is entirely consistent with Cohn's (1866) published diagram. The very thin, membrane-like dorsal edge of the peristome extends for half the total length of the AZM on the left side. These are transparent and easily overlooked. The anterior area displays three frontal and seven ventral cirri. Maupas (1883), Kahl (1932) and Borror (1972) indicated the number of these cirri as 8, 11 and 11, respectively, including

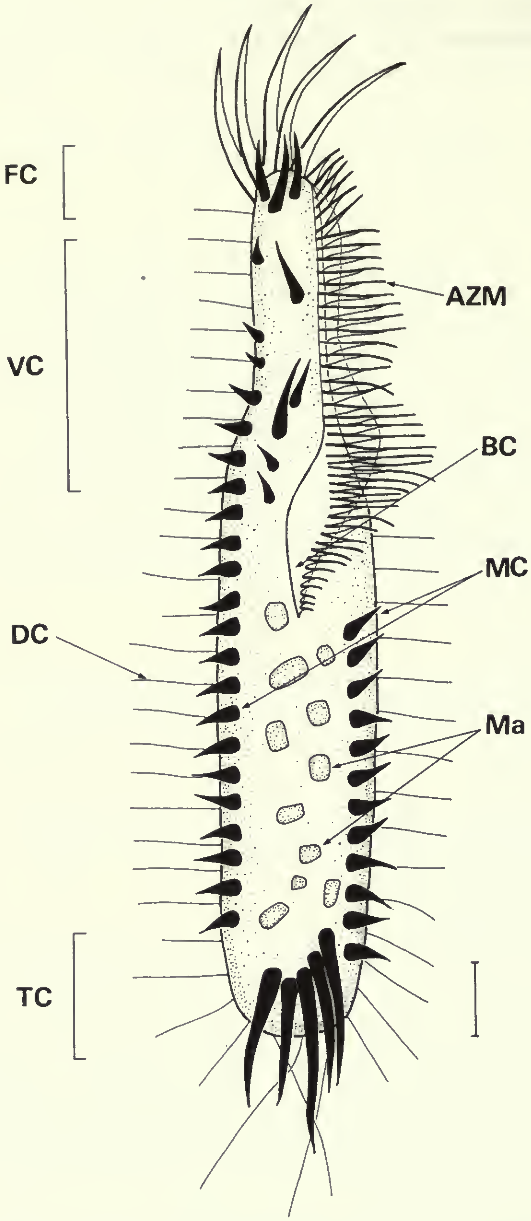

Fig. 1 *Trachelostyla pediculiformis* Entire organism, ventral view, (AZM) adoral zone of membranelles, (FC) frontal cirri, (VC) ventral cirri, (MC) marginal cirri, (TC) transverse cirri, (DC) dorsal cirri, (BC) buccal cavity, (Ma) macronuclei. Bar represents 10 μm.

three distinct frontal cirri. There are no ventral cirri in the middle and posterior of the body as Kahl (1932) described. However in the descriptions of Maupas (1883) and Borror (1972) two ventral cirri just anterior of transverse cirri were present. Five or sometimes six transverse cirri make an oblique row from the left hand to the right hand side of the body. The right marginal cirral row starts from the 'shoulder' adjacent to the apical area and left row runs from just below the buccal region. These two marginal rows are not confluent posteriorly and terminate at the base of the transverse cirri. At both lateral edges rows of very fine and long cilia can be observed, they are particularly long in the posterior region. Maupas (1883) designated these long cilia at the posterior end as caudal cirri, however Kahl (1932) found them projecting from the dorsal surface of the body: that is to say these thread-like cilia of the lateral and posterior are bristles originating from the dorsal side.

Cohn (1866) found this species and appointed the name *Stichochaeta pediculiformis. Maupas* (1883) also described this organism and transferred it to the genus *Gonostomum* as *G. pediculiforme* because he found it had quite different morphological features in the peristome area, and cirral arrangements from the genus *Stichochaeta* of Claparède & Lachmann (1858), Kahl redescribed *G. pediculiforme* in 1928. However, he erected the new genus *Trachelostyla* in 1932 giving the reason that the organism had a 'neck-forming' narrowed peristome area and its two marginal cirral rows were not confluent at the posterior end of the body. He included two species in this genus, *T. pediculiformis* and *T. caudata.* Borror (1972) and Buitkamp (1977) agreed with Kahl (1932) and placed *Gonostomum pediculiforme* and *Stichochaeta pediculiformis* as synonyms of *T. pediculiformis.*

In agreement with Kahl (1932), Borror (1972) and Buitkamp (1977), the possession of a narrowed 'head' area, clearly defined transverse cirri, the non-convergent marginal cirral rows posteriorly and the absence of caudal cirri are sufficient reason to retain this species in the genus *Trachelostyla.* Gourret & Roeser (1888) described *Stichochaeta corsica* as having serried rows of adoral 'cirri', long and fine caudal 'cilia', dorsal 'cilia' and transverse cirri. Careful analysis of their description and diagram reveals the long and fine cilia at the posterior extremity of the body are in reality dorsal bristles, not caudal cirri. From a detailed survey of morphological features it is clear that *S. corsica* must be considered a synonym of *T. pediculiformis.*

Trachelostyla caudata Kahl, 1932

MORPHOLOGICAL DESCRIPTION: Specimens were found in the fine sediments of East-Head, Chichester Harbour, especially in sands which contained a lower content of detrital material than the chosen biotope of *Trachelostyla pediculiformis* (Carey & Maeda, 1985). The dates of sampling and the water temperature of the sampling area were the same as that for *T. pediculiformis.* This psammophilic species was reported to be common in the coastal areas of many European countries and Russia. Locomotion is similar to *T. pediculiformis*, but the 'head region' is not lifted from the substrate during forward movement. The body, 156 µm in length, is fragile and elastic but not contractile (Fig. 2). It is elongated and has a narrowed 'neck-like' anterior and a narrowed 'tail-like' posterior region. The form of peristome area is similar to *T. pediculiformis* which is confined to the left lateral border of the 'head' area, and its posterior bends abruptly, extending backwards to near the centre of the body. Five long membranelles of the AZM are present at the apex of the cell, but the membranelles of the lateral portion are rather short and 'brush-like'. The characteristically long membrane which *T. pediculiformis* possesses in the buccal area is not present in this species. Among the four frontoventral cirri, 3 make a row, but the fourth cirrus from the apex is slightly separated from the other three. The length of these cirri is approximately the same as that of the marginal cirri. There are no frontoventral cirri in the mid- and posterioventral area. Five thick transverse cirri are present, as Kahl (1932) described, these make a oblique row from the left to the right hand side. The right marginal cirral row starts from the base of the narrowed 'head' and the left marginal row begins just posterior of the end of the peristome. The two marginal rows terminate at the base of the transverse cirri. At both the right and left edges of the body, faint dorsal cilia are clearly displayed. These dorsal cilia of the right hand edge run from the top of the apical area, and join the other dorsal row of cilia of the left hand side at the posterior end of the body. Dorsal cilia or cirri are not as long as those of *T. pediculiformis* and do not extend to any great length in the caudal area. There are 8–10 dorsal cirral rows according to Kahl (1932). A contractile vacuole is situated just posterior of the peristome end. In Kahl's (1932) diagram, 11 macronuclei are shown.

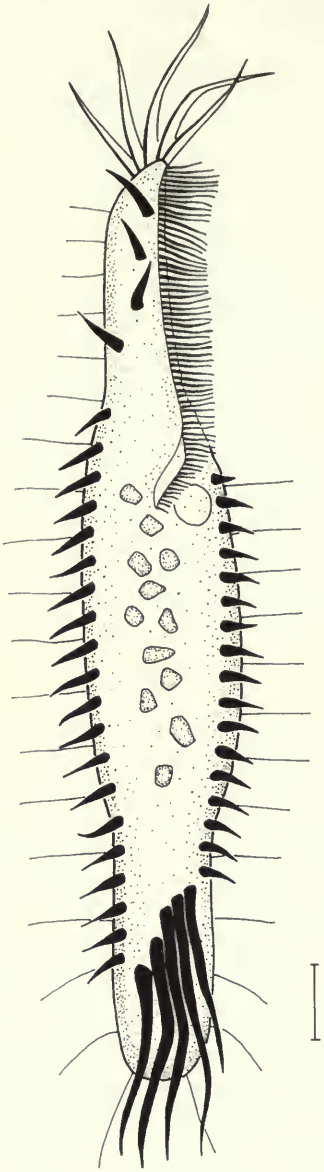

Fig. 2 *Trachelostyla caudata* Ventral view. Bar represents 10 μm.

This animal was originally found in the sands of Kiel by Kahl (1932). In agreement with both Borror (1972) and Buitkamp (1977) this organism has been retained in the genus *Trachelostyla.*

Diagnosis of the Genus *GONOSTOMUM* Sterki, 1878

Oxytricha Stein, 1859 *pro parte*
Plagiotricha Kent, 1881–1882
Stichochaeta Gourret & Roeser, 1888 *pro parte*
Gastrostyla Borror, 1972 *pro parte*
Trachelostyla Borror, 1972 *pro parte*

A genus of hypotrich with a more or less flexible and elastic, but non-contractile body. The body shape is oval or ellipitical, 60–150 µm in length. The peristome area is confined to the lateral border and its posterior portion, in most cases, is abruptly bent towards the centre of the body. The AZM in the apical area is composed of long and thick membranelles. There are 3 distinct frontal cirri in the anterior region. Among the 6 to 20 ventral cirri present, one or two cirri are positioned just anterior of the transversals. No ventral cirri are present in the mid-ventral area. Two to four transverse cirri are present, which are not thickened in most species. There are two marginal cirral rows which are confluent posteriorly, or more correctly run posteriorly to meet several elongate caudal cirri. Dorsal cirri are not long enough to be seen from the ventral side of the body. Two oval macronuclei are present and a single micronucleus is situated near each of the macronuclei. A single contractile vacuole is situated just posterior of the end of the peristome area, at the left hand lateral border. The species belonging to this genus are found in salt water, fresh water and terrestrial soils.

Key to species of *Gonostomum*

1	Ventral cirral rows well developed	2
—	Ventral cirral rows absent	4
2	At least one ventral cirral row extending further than the end of the peristome.	*strenua*
—	Ventral cirral rows terminating at the peristome	3
3	Four transverse cirri present	*affine*
—	Two transverse cirri present.	*algicola*
4	Caudal cirri present	5
—	Caudal cirri absent	*ciliophorum*
5	AZM bent abruptly inwards at the buccal cavity, membranelles large and distinctive . .	*bryonicolum*
—	AZM gently curved inwards at the buccal cavity, membranelles not distinctive. . . .	*spirotrichoides*

Gonostomum affine (Stein, 1859) Sterki, 1878

Oxytricha affinis Stein, 1859
Plagiotricha affinis Kent, 1881–1882
Stichochaeta affinis Gourret & Roeser, 1888
Gonostomum andoi Shibuya, 1929
Gastrostyla affine Borror, 1972
Trachelostyla affine Buitkamp, 1977

DIAGNOSIS: This free swimming species has been found in a variety of habitats including salt water, soil under leaf litter, moss and heathland. The length recorded by Kahl (1932) was 95–115 µm, however those of Wenzel (1953) were measured as 63–125 µm. The body is elongate and its anterior and posterior ends are narrowed and slightly pointed (Fig. 3). Kent (1881–1882) described the body form as lanceolate. The peristome area is arcuate and is confined chiefly to the left lateral side, its posterior end bending inwards at the tip, terminating near the centre of the body. There are three frontal cirri in the anterior area and one buccal cirrus above the paroral membrane. According to Buitkamp (1977) there is one distinct frontal cirrus in the apical region, but Foissner (1982) in his detailed investigation found 3 frontal cirri as Stein (1859), Kent (1881–1882) and Kahl (1932) described. The ventral cirri number 8 to 13 in Stein's (1859) diagram, some of these making a slightly oblique row on the right side of the peristome. There are only 2 ventral cirri in the mid-ventral area, placed just in front of the transverse cirri. Three to five transverse cirri are present, whose length does not extend beyond the posterior end of the body in the original description. However, Kahl (1932), Wenzel (1953) and Foissner (1982) showed this animal having rather longer transverse cirri than those described by Stein (1859). Two marginal cirral rows are confluent posteriorly or terminate as a row of caudal cirri in some descriptions (Wenzel, 1953; Buitkamp, 1977). Two macronuclei are present. A contractile vacuole is situated just below the peristome.

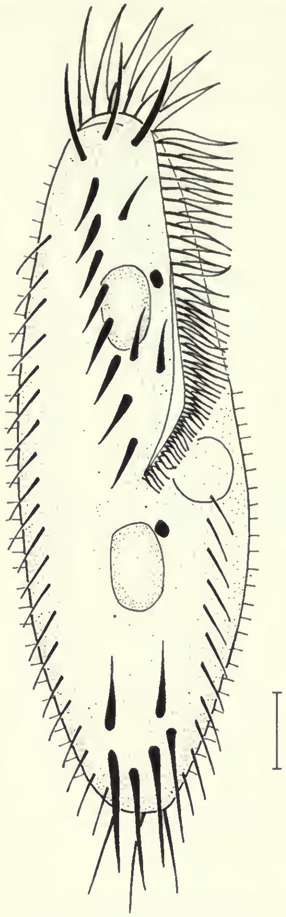

Fig. 3 *Gonostomum affine* After Wenzel, 1953; ventral view slightly modified. Bar represents 10 µm.

This animal was described by Stein (1859) and given the name *Oxytricha affinis.* Sterki (1878) noted the characteristic shape of the peristome area and the lack of mid-ventral cirri. In consequence he erected the new genus *Gonostomum* and transferred *O. affinis* to *G. affine.* Kent (1881–1882) pointed out that the name of *Gonostomum* closely resembled that of *Gonostoma* and *Gonostomus* which were already employed to designate certain genera of fish and molluscs. Consequently Kent appointed the new genus *Plagiotricha* which included *P. affinis*. Gourret & Roeser (1888) agreed with the action of Kent, but chose to transfer *P. affinis* to the genus *Stichochaeta. Gonostomum andoi* Shibuya, 1929 possesses a slightly different arrangement of cirri on the ventral surface from that of *G. affine:* that is, it displays a slightly higher number of frontoventral cirri and no cirri just anterior of transversals. But Kahl (1932) and Buitkamp (1977) showed the variation of form in *G. affine* especially the absence of ventral cirri just anterior of the transverse. Because other features of this organism resemble those of *G. affine,* we designate *G. andoi* as the synonym of *G. affine.* Kahl (1932) retained this organism as *Gonostomum affine* and gave *Gonostomum andoi* as its synonym. Borror (1972) transferred this organism to *Gastrostyla affine* because it possessed one oblique row of ventral cirri. However it is clear that this ventral cirral row in *Gonostomum affine* is not sufficiently developed to ensure removal to the genus *Gastrostyla.* Buitkamp (1977) proposed the new combination *Trachelostyla affine,* however Foissner (1982) retained this species in the genus *Gonostomum.*

In agreement with Kahl (1932) and Foissner (1982), the confluence of the 2 marginal cirral rows (Stein, 1859), the possession of caudal cirri (Wenzel, 1953), the presence of two ventral cirri just anterior of the transversals and 2 macronuclei are sufficient to retain this organism in the genus *Gonostomum*.

Gonostomum strenua (Engelmann, 1862) Sterki, 1878

Oxtricha strenua Engelmann, 1862
Plagiotricha strenua Kent, 1881–1882
Stichochaeta strenua Gourret & Roeser, 1888

DIAGNOSIS: This organism has a flexible and contractile form, the body being elongate and elliptical (Fig. 4). It has been described from fresh water. The length recorded by Engelmann was 150 µm. Its anterior and posterior ends are evenly rounded. The frontal region is slightly thinner and dorsoventrally thicker than the posterior area. The peristome area is very narrow and confined to the left hand lateral edge, its posterior end being inwards, extending nearly to the centre of the body. The adoral zone of membranelles in the lateral area of the peristome is longer than that of *Gonostomum affine.* There are 23–25 frontoventral cirri, most of which form two slightly oblique rows, one row extending two thirds of the total body length, the other row being only half as long. No frontoventral cirri are present in front of the 4 transverse cirri. We assume that among the transverse cirri, possibly two can be counted

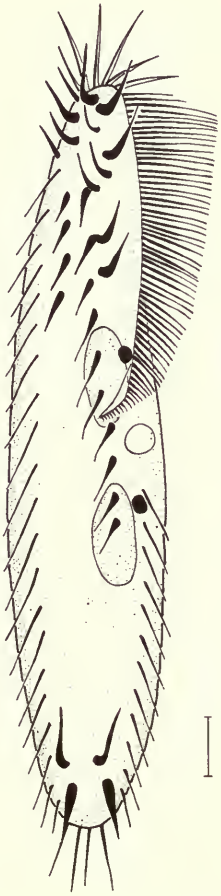

Fig. 4 *Gonostomum strenua* After Englemann, 1862; ventral view. Bar represents 10 µm.

as frontoventrals. The right and left marginal cirri were confluent posteriorly. At the posterior extremity there were 4 long, fine caudal cirri. Two macronuclei are present in the midventral area and one contractile vacuole is situated just below the peristome.

Englemann (1862) first described this organism under the name *Oxytricha strenua*. Sterki (1862) established the new genus *Gonostomum* and transferred *O. strenua* to *G. strenua* on the same basis that *O. affinis* was transferred to *G. affine* (see species description, *G. affine*). Kent (1881–1882) erected the new genus *Plagiotricha* and proposed *P. strenua,* and Gourret and Roeser (1888) transferred this organism to *Stichochaeta strenua.* Kahl (1932) and Stiller (1974) redescribed it as *G. strenuum* and *G. strenua,* respectively. Borror (1972) retained only *G. strenua* in the genus *Gonostomum* and adopted *Oxytricha tricornis* Milne, 1886–1887 as its synonym. After careful study of the original description and diagram of *O. tricornis* it is clear that it should be excluded from *Gonostomum* and from *Oxytricha* because of the unusual form taken by peristome.

Gonostomum algicola Gellért, 1942

Trachelostyla canadensis Buitkamp & Wilbert, 1974
Trachelostyla affine Buitkamp, 1977.

Diagnosis: This species was found in association with green plants on rocks, feeding on flagellates. The length has been recorded as 60–100 µm. The body displays an oval or elliptical shape (Fig. 5). The peristome area is confined to the left lateral border and the AZM

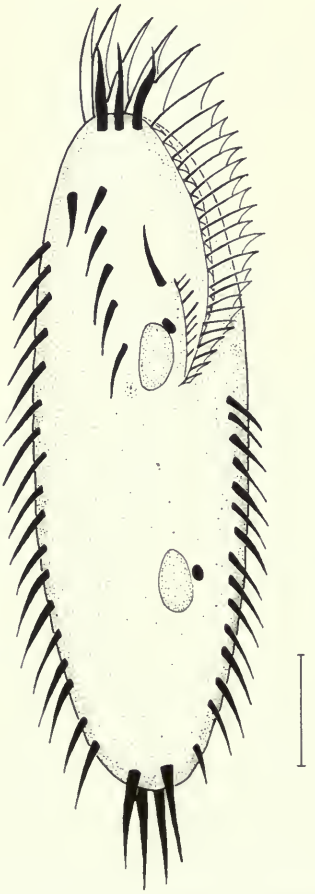

Fig. 5 *Gonostomum algicola* After Gellért, 1942; ventral view. Bar represents 10 µm.

extends backwards to nearly half the body length. A quarter of the peristome is bent inwards toward the body. In the frontal area 10 thick cirri are usually observed, including 3 frontal cirri and 1 buccal cirrus. Five ventral cirri make a slightly oblique row in the frontal region. Mid-ventral cirri are absent. Transverse cirri number two and there are two caudal cirri present. There are 15 left marginals and 18 right marginals. Two macro- and two micronuclei are present. These features are characteristic of the genus *Gonostomum.*

Buitkamp and Wilbert (1974) isolated *Trachelostyla canadensis* from prairie soil in Canada. Buitkamp (1977) transferred this species to *T. affine* in his revision of the genus *Trachelostyla.* The presence of 3 frontal cirri, 1 buccal cirrus, 2 transverse cirri and 2 macronuclei, also the lack of ventral cirri in the mid-ventral area indicate this species has a strong similarity to that of *Gonostomum algicola* although there are 2 caudal cirri instead 3 in *G. algicola.* These taxonomic features are clearly sufficient to designate this animal as the synonym of *G. algicola.*

Gonostomum spirotrichoides Gellért, 1956

Trachelostyla spirotrichoides Borror, 1972
Trachelostyla affine Buitkamp, 1977

Diagnosis: This species has been found in soil under moss, feeding on bacteria and detritus. The body length is 110 µm and its form is elongate and cylindrical (Fig. 6). The peristome

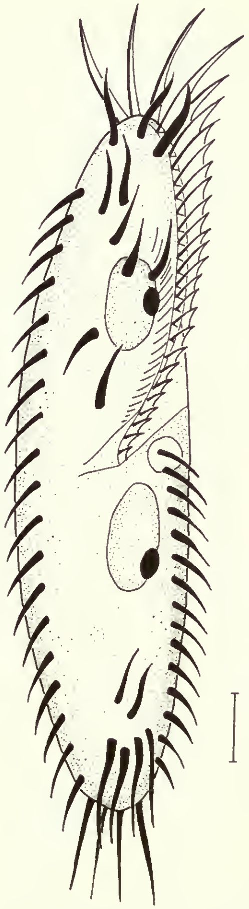

Fig. 6 *Gonostomum spirotrichoides* After Gellért, 1956; ventral view. Bar represents 10 µm.

region is confined to the left lateral edge and extends backwards to nearly the centre of the body. The AZM comprises 27 membranelles of which 4 membranelles in the apical area are distinctly longer than others. The buccal opening is situated at the posterior extremity of the AZM, which displays a funnel like appearance. There are 3 distinct frontal cirri at the apex of the cell. Among the five ventral cirri present, three cirri are arranged in one oblique row extending from the right to the left of the body. It is not certain whether one cirrus which is situated below the end of this cirral row, is a buccal cirrus. Two isolated cirri are present at the region just below the majority of the ventrals and there is another pair of ventral cirri just in front of the 4 transversals. The number of right marginal cirri is 19, left marginal cirri number 15. Between the two marginal cirral rows there are four caudal cirri situated at the posterior. On the dorsal surface, three cirral rows of long bristles have been described. Two macronuclei with one micronucleus are present at the fronto- and midventral areas, respectively. A contractile vacuole is situated at the left of the posterior end of the AZM.

Because of the possession of caudal cirri, the presence of two ventral cirri just anterior of the transversals and two macronuclei, Borror (1972) was clearly in error in attributing this animal to the genus *Trachelostyla,* as *T. spirotrichoides.* Buitkamp's (1977) designation of the new combination *Trachelostyla affine* is also incorrect. Based on the present study this species has been retained in the genus *Gonostomum*, as *G. spirotrichoides.*

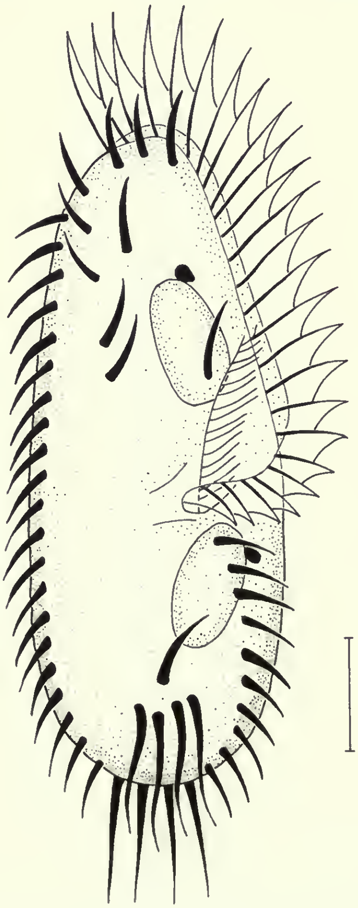

Fig. 7 *Gonostomum bryonicolum* After Gellért, 1956; ventral view. Bar represents 10 µm.

Gonostomum bryonicolum Gellért, 1956

Trachelostyla bryonicolum Borror, 1972
Trachelostyla affine Buitkamp, 1977

DIAGNOSIS: The ciliate was found in the humus layer of soil samples and has been designated a detritus feeder, 60 µm, in length. The body is oval, cylindrical and the peristome region is arcuate and confined chiefly to the left lateral border, consequently its posterior end bends abruptly inwards, terminating near the centre of the body where the buccal apparatus is situated (Fig. 7). In the anterior region there are 3 distinct frontal cirri and 4 ventral cirri, behind which are a separate pair of ventral cirri. One buccal cirrus is situated just above the anterior-most end of the paroral membrane. There is only one ventral cirrus in the midventral area, placed just in front of the four transverse cirri. Two marginal cirri rows terminate as a group of four caudal cirri at the posterior. Four cirral rows of long bristles on the dorsal side have been described. Two macronuclei are present together with one micronucleus, and one contractile vacuole is situated near the termination of the peristome.

Borror (1972) and Buitkamp (1977) transferred this species to the genus *Trachelostyla* as *T. bryonicolum* and *T. affine,* respectively. The existence of caudal cirri and a ventral cirrus just anterior of the transversals, indicate that it should be retained in the genus *Gonostomum* as *G. bryonicolum.*

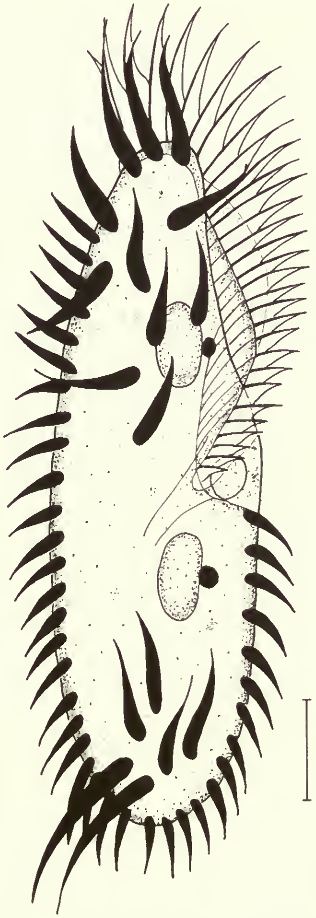

Fig. 8 *Gonostomum ciliophorum* After Gellért, 1956: Ventral view. Bar represents 10 µm.

Gonostomum ciliophorum Gellért, 1956

Trachelostyla ciliophorum Borror, 1972
Trachelostyla affine Buitkamp, 1977

DIAGNOSIS: This species has been described as a bacteria and detritus feeder, and was found in the humus layer of soil. The body, 70 µm in length, displays a slender and oval form (Fig. 8). The peristome area is confined chiefly to the left lateral border, its posterior portion bending inwards into the body. The buccal apparatus is located at the posterior end of the AZM. Three distinct frontal, one buccal and seven ventral cirri are present on the right of the peristome. There are two ventral cirri in the posterioventral area placed just anterior of the transverse. There are four transverse cirri, two of which were longer than the others. Two marginal cirral rows are confluent posteriorly where no caudal cirri are situated. Two macronuclei with one micronucleus are present, one at the front and the other in the midventral area.

Without detailed comments, Borror (1972) transferred this species to the genus *Trachelostyla* as *T. ciliophorum* and Buitkamp (1977) proposed the new combination *Trachelostyla affine,* again with scant information. Here it has been retained in the genus *Gonostomum*, as *G. ciliophorum* despite the revision of Borror (1972) and Buitkamp (1977) who clearly did not take into account the presence of confluent marginals and other diagnostic features.

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Notes on Atlantic and other Asteroidea. 4. Families Poraniidae and Asteropseidae

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Introduction

The skeletal structure of the poraniid starfishes, upon which the classification relies, is hidden or at least obscured by the more or less thickened body wall and opaque skin. X-radiographs of some North Atlantic specimens have thrown new light on the limits of several taxa. The study has been helped by additional material, from various museums and oceanographic institutes, notably from recent collections of the *Discovery,* RSS *Challenger, Walter Herwig* and *Alvin,* as well as many type specimens. Two inter-family transfers of genera are also made: the Southern Ocean genus *Poraniopsis* Perrier—hitherto placed in the Echinasteridae despite its name—is now included in the Poraniidae while conversely *Poraniella* Verrill is transferred from the Poraniidae to the Asteropseidae. In view of previous confusion between these two families, the paper is prefaced by full diagnoses of both. A tabular key for characters of the genera of Poraniidae is appended.

Systematic Account

Family *ASTEROPSEIDAE* Hotchkiss & Clark

Asteropsidae Perrier, 1884: 154.
Gymnasteriidae (pt) Sladen, 1889: 355–356; Perrier, 1894: 327.
Asteropidae Fisher, 1908: 90; 1911 (pt): 247–248; Verrill, 1915: 86.
Poraniidae (pt) Spencer & Wright, 1966: U69.
Asteropseidae Hotchkiss & A. M. Clark, 1976: 266; Blake, 1980: 179; 1981: 381, 391.

A family of the order Valvatida with body form stellate, but the young nearly pentagonal, interradial arcs rounded or sometimes with a blunt angle; arms normally five, flat below, convex or carinate above, there being a distinct ventrolateral angle, entirely covered by more or less thickened skin, opaque and tending to obscure the skeleton in larger specimens, $R > 20$ mm; abactinal skeleton with primary calycinal plates usually distinguishable, small specimens with compact, flat, initially rounded or hexagonal somewhat imbricating plates (as in the Atlantic genus *Poraniella* which is only known at $R < 20$ mm) arranged in longitudinal series but becoming an open reticulum with linking secondary plates, armed with single carinal spines only (*Asteropsis*), spaced fine spines (*Poraniella*), numerous spines (*Valvaster)* or completely spineless (other genera); abactinal papulae single in small specimens but becoming grouped in the skeletal meshes in larger ones; marginal plates well developed, inferomarginals thick wedge shaped, usually projecting to form a ventrolateral angle, variously armed to match the abactinal armament (*Poraniella* with a horizontal fringe of divergent spines along the edge and a few smaller ones above), superomarginals usually bare and more or less inset but with a few small spines in *Poraniella* or with multiple spines and often a conspicuous pedicellaria in *Valvaster*; actinal plates in longitudinal series parallel to the ambulacra, the largest plates and longest series adradial, naked or armed with a few spaced spines; adambulacral plates with two series of spines sheathed in thick skin: pedicellariae present in some species, granuliform or (in *Petricia* and *Valvaster*) large bivalved

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(*Valvaster* also having some elongated tong shaped ones): internally interbrachial septa present and reinforced by a proximal vertical calcified column in each interradius, joined to the side wall of the disc by a membrane (in *Asteropsis* at least; septum present but undescribed by Fisher, 1911 in *Dermasterias* and in *Valvaster* by Blake, 1980).

DISCUSSION: In distinguishing between the Asteropseidae and Poraniidae in 1976, Hotchkiss & Clark (p. 266) failed to realize that *Poraniella* Verrill, 1914 (then unrepresented in the British Museum collections) shares the arrangement of the series of actinal plates parallel to the furrow characteristic of the Asteropseidae, to which this west indian genus is now referred from the Poraniidae as the only Atlantic representative of an otherwise Indo-Pacific family. All the known specimens of *Poraniella* are small, whereas the other asteropseids may exceed 70 mm or even 100 mm R.

In comparison of a *Poraniella echinulata* (Perrier) (from the *Pillsbury* collections in the Lesser Antilles) with a small *Asteropsis carinifera* (Lamarck) (from the Indian Ocean), both R *c.* 10 mm, the abactinal plates are similarly arranged in longitudinal rows and hexagonal in shape, though with slightly better developed and more imbricating lobes in *Poraniella* where there is a well developed armament of fine spaced spinelets or spines on the abactinal, marginal and actinal plates missing in the *Asteropsis.* Both have the five primary radial plates distinctly enlarged at the head of the midradial series of plates which form a keel in the *Poraniella* whereas, surprisingly, the rays are quite flat in the small *Asteropsis* though keeled in larger ones. Also the superomarginals of the small *Asteropsis* completely overlie the inferomarginals, rather than being inset as in *Poraniella,* and each bears a relatively stout tubercular spine and some smaller tubercles, though in large *Asteropsis* these plates are inset and usually naked. The skin investment is thicker throughout in the *Asteropsis* but the wet preservation (the *Poraniella* is dry) may account for the difference.

Because of the general resemblance of the plating at some stage of the ontogeny, I do not think that the difference in armament and apparently thinner skin in the *Poraniella* merit more than a generic difference, justifying its inclusion in the Asteropseidae. Indeed, *Poraniella* is intermediate in armament and skin between *Asteropsis* and *Valvaster,* supporting Blake's inclusion of *Valvaster* in the family in 1980.

Family **PORANIIDAE** Perrier

Poraniidae Perrier, 1893: 849; 1894: 163–164; Verrill, 1914: 17; 1915: 68; Mortensen, 1927: 89–90; Fisher, 1940: 154; Spencer & Wright, 1966 (pt): U69; Hotchkiss & Clark, 1976: 263–266; Blake, 1981: 380–381.
Gymnasteriidae: Bell, 1893: 21, 78; Farran, 1913: 16.
Asteropidae (pt) Fisher, 1911: 247–248.
Asteropidae: Koehler, 1921: 40–41; Mortensen, 1933: 249: Fisher, 1940: 136.

A family of normally five-rayed Valvatida with body form short-rayed stellate or almost pentagonal, interradial arcs rounded, or sometimes angular (in *Poraniopsis* and some *Poraniomorpha*); upper side arched, under side flat or, if the body is cushion shaped, slightly convex, a ventrolateral angle more or less distinct; dorsal body wall thickened and skin opaque in all but the smallest specimens; abactinal plates obscured or concealed, when well developed either similar and forming an irregular fairly compact reticulum (*Poraniomorpha*) or with the ten primary calycinal plates on the disc enlarged and making a pentaradiate pattern from which run irregular carinal (midradial) series of plates linked to the superomarginals by transverse chains of dorsolateral plates sometimes interconnected to form an open reticulum with larger nodal plates (*Porania* and *Poraniopsis*), but in some taxa the plates progressively resorbed internally, even completely lost in large specimens, R> 50 mm, and the body wall more or less thickened to give compensatory support, gross armament usually lacking or sparse, only *Poraniopsis* and occasional *Porania* with coarse spaced spines on some of the larger plates, sometimes the skin of the upper side with more or less numerous spiniform, papilliform or almost granuliform spinules, forming a continuous coating, rarely even finer spicules, this superficial armament not necessarily penetrating the soft tissue to contact the underlying plates; papulae either spaced or clustered, often present intermarginally as well as abactinally; marginal plates either well developed together with the abactinal skeleton (though often becoming hollow) or sharing in general decalcification, when well developed the two series tending to alternate and often flattened in planes at right angles, the inferomarginals then horizontal and alone supporting the venterolateral angle, the superomarginals vertical (e.g. in *Porania*) or both series more compact, blocklike, sharing in forming the ambitus, the angle less well marked (*Poraniomorpha*), or the plates relatively undistinguished except for their longitudinal arrangement, the inferomarginals ventrally aligned and without a distinct angle (*Poraniopsis*), inferomarginals armed with a horizontal series, sometimes enclosed within the body wall or more or less aborted (*Porania* and *Chondraster*), or with multiple spinules usually enlarged into spinelets along the maximum convexity (*Poraniomorpha*), or with a few coarse spines not forming a horizontal series (*Poraniopsis*); actinal areas large, the plating obscured by thick skin usually with spaced grooves which sometimes fork or anastomose running from furrow to margin, or pustular, the underlying plates primarily arranged in arcs parallel to the margin, the longest series admarginal (abradial), the shortest adoral, spanning the interradius, also forming series corresponding to the grooves, if the skeleton is generally reduced then the actinals are progressively resorbed from within, appearing as rings on the inner face of the body wall of dissected specimens, the last traces of them close to the adambulacrals, actinal surface either naked or armed with a few spaced spines arising from the underlying plates tending to form series parallel to the margin, or with spinelets enlarged from spinules, spinules alone or unarmed; adambulacrals armed with a few sheathed furrow and subambulacral spines, aligned either transversely (e.g. *Porania*) or longitudinally (*Chondraster* and *Poraniomorpha*); pedicellariae unknown; internally interbrachial septa developed, reinforced by vertical plating unless the entire skeleton is reduced.

Discussion: Hotchkiss (in Hotchkiss & Clark, 1976: 265–266) was largely responsible for emphasizing the importance of the different arrangement of the actinal plates with the primary series either parallel to the margin as in the Poraniidae, or parallel to the furrow as in the Asteropseidae. The two families are also probably distinguishable by thermal differences since the Asteropseidae are found in shallow water in tropical or warm-temperate seas while the Poraniidae are mainly from cold temperate and boreal seas, only occurring in lower latitudes at greater depths and with a stunted form. This accords with the removal now from the Poraniidae to the Asteropseidae of the west indian *Poraniella* Verrill, 1914, because of the actinal plating, which is known from a minimum depth of only 20 m compared with *c.* 175 m for *Marginaster pectinatus* Perrier, the only poraniid from the same area.

Observation of this same character, agreeing conversely with the Poraniidae, in the genus **Poraniopsis** by Blake (pers. comm.) prompted him to suggest that it be removed from the Echinasteridae to this family. Perrier (1891: K106–107) failed to describe the arrangement of the actinal plates but Madsen (1956: 29) noted that their spines run parallel to the margin. Perrier thought *Poraniopsis* intermediate between *Echinaster* and *Porania,* emphasizing this by using *echinaster* as a specific name for the type species. Although he cited more characters in which *Poraniopsis* resembles *Porania,* more weight must have been given to those such as arm shape shared by *Echinaster*. Fisher (1911: 261) thought that resemblances to *Porania* are 'mostly superficial', holding to this view still in 1940 (pp. 154–155) when faced with an unusually well-armed Falkland Is specimen of *Porania antarctica* (Fig. 1B). However, I find there are also important internal characters in which *Poraniopsis* agrees better with *Porania* than with *Echinaster*, comparing specimens from the vicinity of southern South America, as summarized in Table 1. The abactinal plating is very similar, with the primary calycinal plates forming a pentaradiate pattern on the disc in both and irregular midradial (carinal) series forming part of an open reticulum; some nodal plates bear large spines and there are often superficial spinules in the skin. The latter are better developed in the truly antarctic subspecies *P. antarctica glabra* though minute ones *c.* 0·25 mm long are present

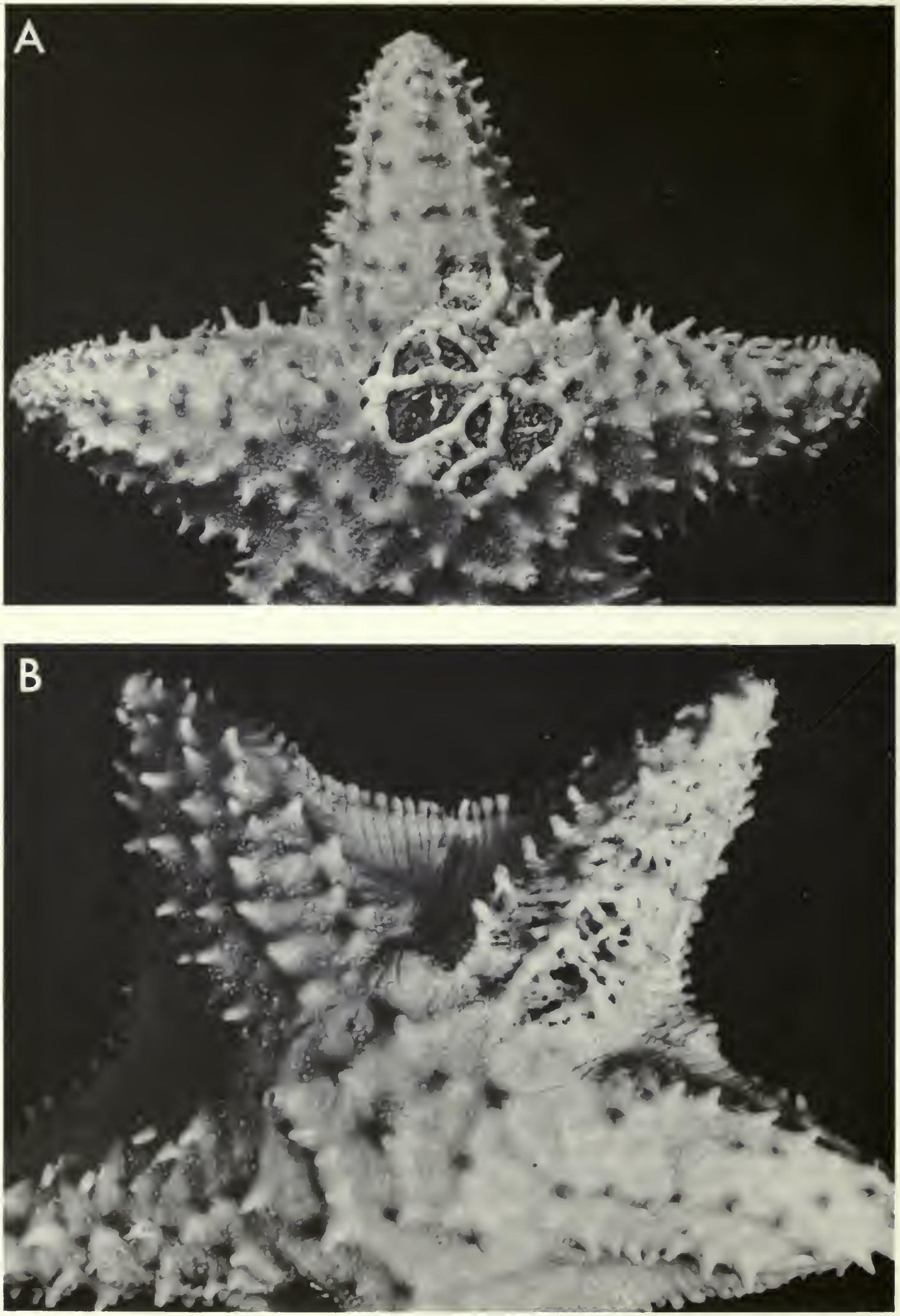


Fig. 1 A. *Poraniopsis echinaster* Perrier, BM reg. no. 1975.11.12.9, Chinquihue, S Chile, R 36 mm; dry, partly denuded, showing spinules between the spines. × 2. B, *Porania* (*Porania*) *antarctica magellanica* Studer, 1948.3.16.448. *Discovery* Investigations st. 80, Falkland Is, R 60 mm; wet, showing papulae between the spines, the spinules microscopic. × 1½.

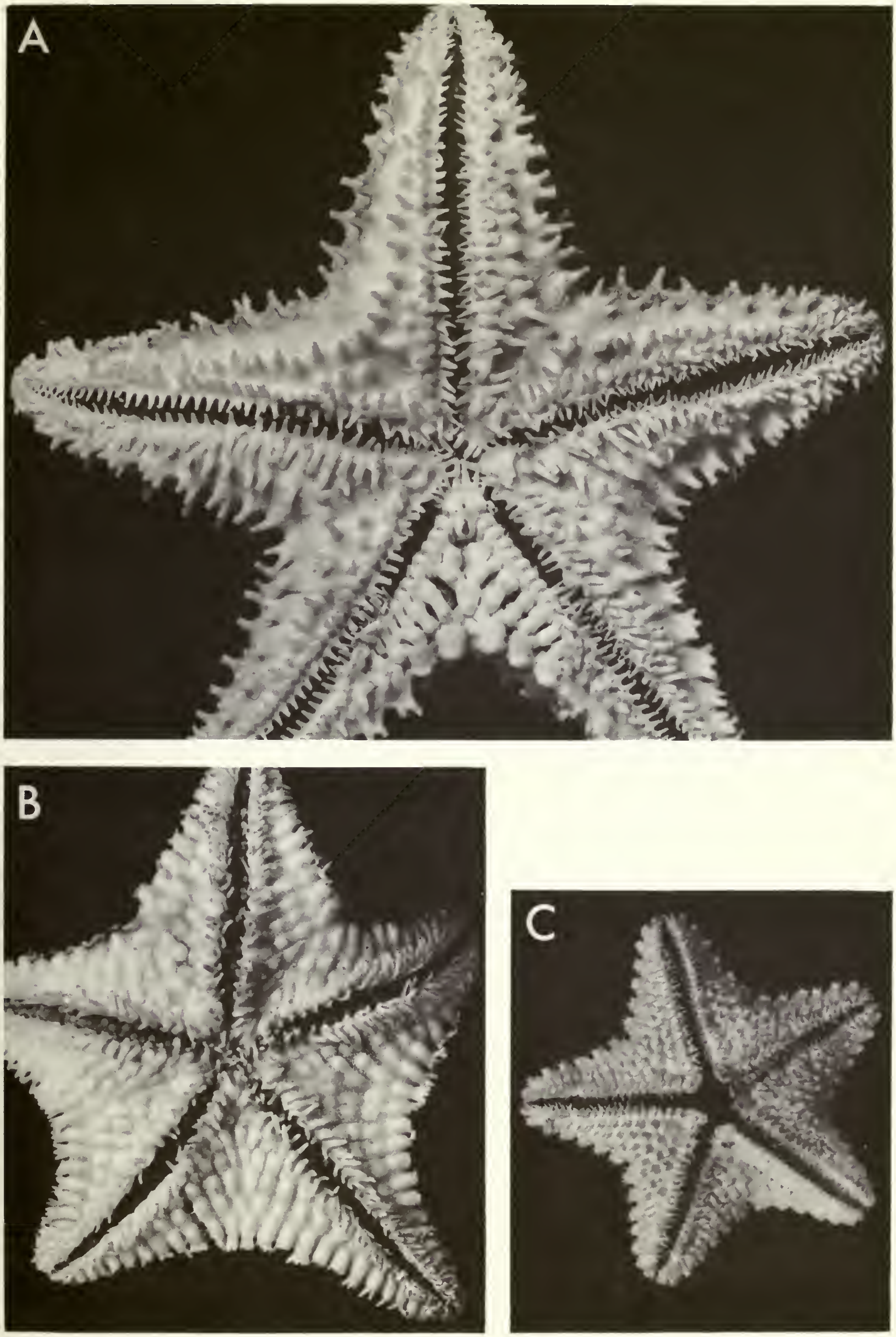


Fig. 2 A, *Poraniopsis echinaster* (as in 1A), partly denuded. ×2. B, *Porania* (*Porania*) *pulvillus* (O. F. Müller), 1922.4.10.1, Lousy Bank, SW of Faeroe Is, R *c.* 36 mm; wet but contracted, the contours of the plates showing their limits. ×1½. C, *Poraniella echinulata* (Perrier), *Pillsbury* st. 853, Windward Is, R 10 mm; dry, partly denuded. ×3.

Table 1 Comparison of *Poraniopsis* with *Porania* (especially *P. antartica*) and *Echinaster*. Agreement with *Porania* in capitals.

	Porania	*Poraniopsis*	*Echinaster*
1	r	a	a
2	C	C	I
3	S	S	N
4	d	u	u
5	a	r	r
6	M	M	L
7	D	D	S

1. Interradial arcs:
   a angular
   r rounded
2. Primary calycinal plates:
   C conspicuous when denuded, linked to form a pentaradiate pattern
   I inconspicuous
3. Skin:
   S usually containing a fine superficial secondary armament of small scattered spinules independent of the underlying plates
   N nude, armament limited to spines mounted on the plates
4. Superomarginal plates:
   u relatively unspecialized, similar to the abactinal plates though corresponding in number to the inferomarginals; usually armed with one or more spines
   d distinct from the abactinals; spineless
5. Profile of ambitus (widest part of body):
   r rounded, curving into the upper and lower sides; inferomarginals inset somewhat on the ventral side, their spines not forming a continuous fringe
   a angular, the prominent ventrolateral angle emphasized by a prominent fringe of spines
6. Alignment of actinal plate series and any coarse armament:
   M in arcs across the interradii parallel to the margin, the admarginal series the longest
   L in longitudinal lines along each ray parallel to the furrow, the adradial series the longest
7. Adambulacral plate joint faces:
   D with a deep restricted interadambulacral muscle depression towards the furrow face
   S with a shallow extensive muscle depression.

Characters 6 and 7 carry the greatest weight in my opinion.

in the Falklands specimen. There is also frequent alternation of the plates of the two marginal series of both *Poraniopsis* and *Porania* and the adambulacral spines are very few, thickly sheathed in skin and aligned at right angles to the furrow, besides the most obvious resemblances of the thick opaque skin and the actinal plate arrangement. Sectioning of an arm shows that the proximal face of the adambulacral plates in *Poraniopsis* has a similarly deep interadambulacral muscle depression towards the furrow side to that found in the poraniids examined, quite different from the much wider and more shallow depression in *Echinaster* (see Blake, 1981, fig. 2, *Chondraster* and *Echinaster*, also Figs 7, 8 here). The main differences in *Poraniopsis* consist of the better-defined rays with an angular rather than curved-interradial arc, the resemblance in shape and armament of the superomarginal plates to the primary (nodal) abactinals and the absence of a distinct ventrolateral angle, the inferomarginals having no horizontal abradial prolongation being instead slightly inset ventrally with the spines of consecutive plates quite discrete, not forming a continuous horizontal fringe. Although the diagnosis of the Poraniidae needs to be somewhat modified to accommodate it, the balance of evidence, I believe strongly supports the inclusion of *Poraniopsis*. Madsen (pers. comm.) tells me that Mortensen placed *Poraniopsis* in the Asteropidae (then including Poraniidae) in the MS catalogue of asteroids in the Zoological Museum, Copenhagen, giving a clue to this disposition by placing *Poraniopsis* after *Chondraster elattosis*, well separated from the Echinasteridae in his table of south african echinoderms (1933: 225). Leipoldt (1895) also concluded that *Poraniopsis* belongs in the Poraniidae but this has generally been overlooked.

Ten other nominal genera of poraniids are known from Atlantic waters. With the currently accepted name of the type species, these are:

Porania Gray, 1840. *P. pulvillus* (O. F. Müller, 1776) (as *Asterias*)
Poraniomorpha Danielssen & Koren, 1881. *P. hispida* (M. Sars, 1872) (as *Asterina*)
Tylaster Danielssen & Koren, 1881. *T. willei* Danielssen & Koren, 1881
Marginaster Perrier, 1881. *M. pectinatus* Perrier, 1881
Chondraster Verrill, 1895. *C. grandis* (Verrill, 1878) (as *Porania*)
Culcitopsis Verrill, 1914. *C. borealis* (Süssbach & Breckner, 1911) (as *Culcita*)
Poranisca Verrill, 1914. *P. lepidus* Verrill, 1914
Pseudoporania Dons, 1936. *P. stormi* Dons, 1936
Sphaeriaster Dons, 1939. *S. berthae* (Dons, 1938) (as *Sphaeraster*)
Spoladaster Fisher, 1940. *S. brachyactis* (H. L. Clark, 1923) (as *Cryaster*).

Two of these, **Marginaster** and **Poranisca,** are only known from small specimens, R<20 mm. Verrill (1914: 19) suggests that *M. pectinatus* is probably 'simply the young of *Porania* or some similar genus', while his own *Poranisca* was proposed 'as a matter of convenience for another group of small young forms belonging to this family, until they can be connected with adults'. However, Downey (1973: 81) found some of the small Marginasters from the West Indies to be sexually mature. It is not clear from Verrill's account just how he thought *Poranisca lepidus* differs from *Marginaster.* His photograph of the largest (syn) type (1914, pl. 1, fig. 3a) is remarkably similar to the specimen of *M. pectinatus* figured by Downey (1973, pl. 37, fig. A). Both have fairly numerous coarse abactinal spines. Verrill wrote: 'the type is from off the eastern coast of the United States, in 77 fathoms, no, 18,485, Nat. Mus.' A specimen with this catalogue number sent to me as a 'Type' of *Marginaster austerus* Verrill, 1899, was originally so identified by Verrill but subsequently he wrote '*Por. lepidus* V. Type' on the back of the earlier label. This label also bears in pencil an illegible *Albatross* station number beginning with 2 over which has been written 'near sta. 2265' the full station data for which are: 37°07′40′′N, 74°35′40′′W (off Chesapeake Bay) 70 fathoms. Since in 1899 (p. 222) *Marginaster austerus* was cited as from *Blake* and *Albatross* stations in *the West Indies* [my italics], in which area many hauls numbered at around 2350 were made, I think it very likely that the substituted number and hence the more northern type locality given for *P. lepidus* were misleading. It is significant that Verrill included no less than eight figures of *Poranisca lepidus* in his 'Starfishes of the West Indies' (1915) without having any mention of the species in his text, while the 'east of the U.S.' locality should have made it completely inappropriate. His plate, 4, fig. 3 shows this specimen, although it was not among the four illustrated in 1914 (pl. 1, fig. 3a-d) some of which have relatively broader inferomarginal plates, leaving little doubt that *lepidus* is a synonym of *Marginaster pectinatus. Poranisca* therefore becomes a synonym of *Marginaster.*

A second *Albatross* specimen in the U.S.N.M. collection labelled as a 'type' of *Marginaster austerus* (cat. no. 10179 from st. 2333, 'off Havana, Cuba, 169 fathoms') proved to be a *Poraniella echinulata* (Perrier, 1881), the actinal plates being aligned parallel to the furrow and the five primary radial plates being conspicuously enlarged and convex. Little, if anything of Verrill's 1899 description of *austerus* could have been based on this specimen.

The only other extant 'type' of *M. austerus* is in the Peabody Museum, Yale (no. 9858) labelled by Verrill 'sta. unknown. West Indies. coll. A.E.V. Two enlarged photos; also drawings'. This has R/r 16–17/10 mm (17/11 according to Verrill, 1915: 78) and is almost certainly the specimen with an abbreviated arm shown in his pl. 3, fig. 1, 1a, captioned as 'type'. Most of his 1899 description (p. 221) could have been based on it except for descriptions of the primary calycinal plates as *distinctly* enlarged and the proximal actinal plates as bearing rows of spinules—both contradicted in his 1914 and 1915 remarks, the latter specifically referring to the type. Accordingly, this specimen is the most appropriate one for selection as lectotype. Superficially it looks rather different from *Marginaster pectinatus* (compare Figs

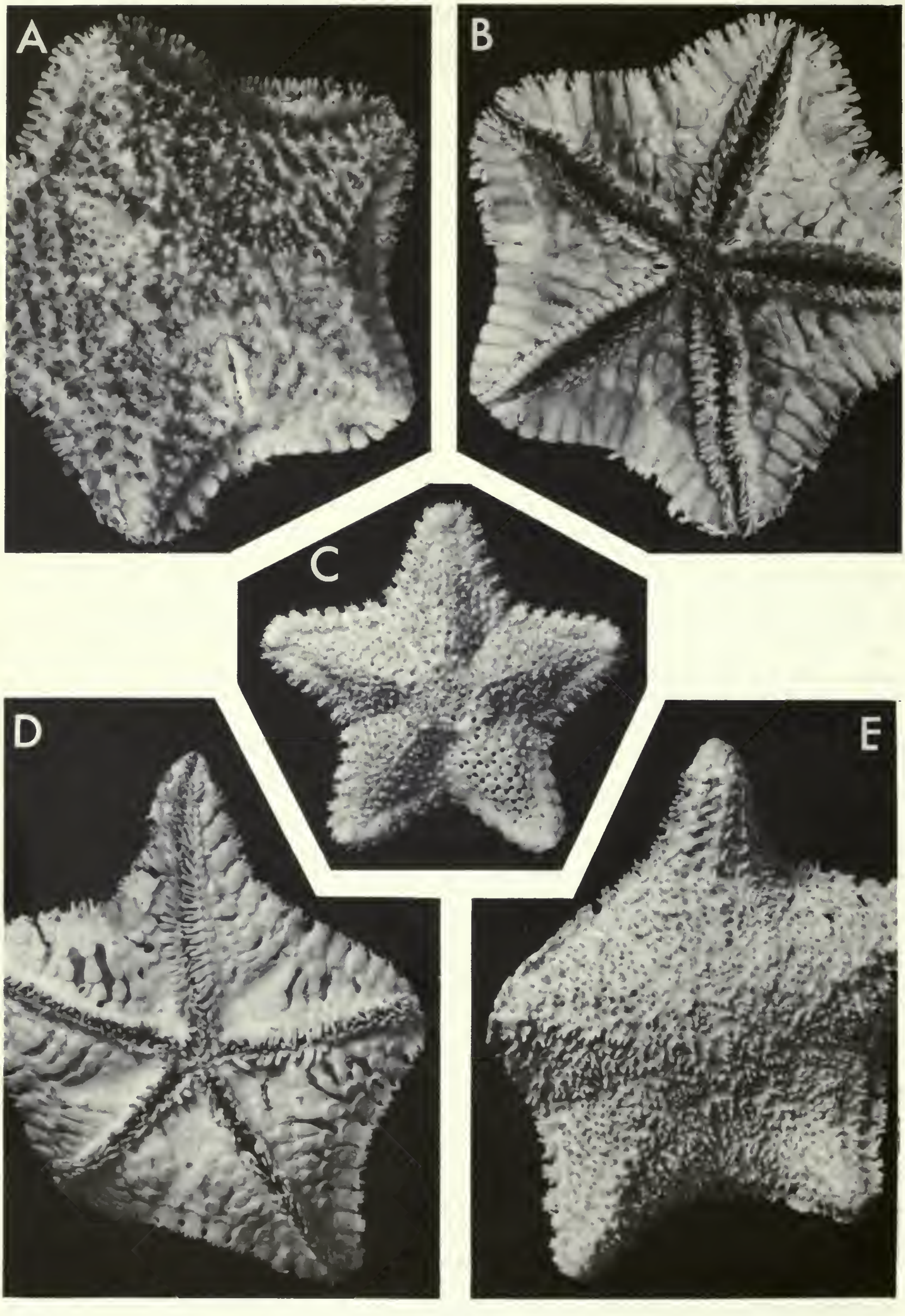


Fig. 3 A, B, *Marginaster pectinatus* Perrier, *Pillsbury* st. 876, Windward Is, R 15 mm; dry, partly denuded. C, *Poraniella echinulata* (as in 2C), dorsal view. D, E, *Marginaster austerus* Verrill, P. M. Yale no. 9858, lectotype, 'West Indies', R 16–17 mm; dry. All × 3.

2C, 3C and 3A, B) notably in the more evenly convex upper side after drying—all the dried *pectinatus* seen being almost flat level with the tops of the superomarginal plates; also the number of marginals is greater, 8–10 rather than 7 or 8 in *pectinatus* of similar size and the inferomarginals project less, forming only an inconspicuous border in ventral view; lastly, the superomarginals in *austerus* are armed with spaced spines for their full height, not just at the upper end, whereas *pectinatus* usually has a bare belt above the inferomarginals, only occasionally a few longer superomarginal spines. The first of these differences may be attributable to an artefact of preservation but the others together could provide a significant difference. However, in general the remaining armament is similar and I suspect that *austerus* will prove to be a synonym of *pectinatus* when more material is available. It should be noted that Verrill's pl. 11, fig. 6a (1915) misrepresents the adradial actinal plates as being in line with the furrow; they are parallel to the margin as usual in poraniids.

There is a further possibility that *Marginaster* itself could be a synonym of *Porania,* to which genus Verrill provisionally referred *austerus* in 1914 (p. 20). In 1895 (pp. 138–139) he wrote of *P. insignis* from east of the U.S.A. 'Young specimens––have more or less numerous small, scattered simple spines, both on the dorsal and ventral plates; these plates are distinctly visible, beneath the cuticle, when dried, and the upper marginal plates are relatively larger than in the adult. The papulae are few and scattered. In this stage, it agrees in all respects with the genus *Marginaster* Perrier and *Lasiaster* Sladen, both of which are probably the young of *Porania* or *Poraniomorpha*'. Possibly *Lasiaster* was added here as an afterthought, since he used the singular 'genus'; it has since been synonymized with *Poraniomorpha.* A proper comparison of *M. pectinatus* with small Poranias from off the USA may shed more light on the relationship and the status of the name *Marginaster.*

As for the even smaller (R max. *c.* 10 mm) geographically 'fringe' species (latitudinally). *Marginaster capreensis* (Gasco, 1876: 38) from the Mediterranean in 50-*c.* 600 metres this is very similar in abactinal and marginal armament to *M. pectinatus* but has more numerous actinal and adambulacral spines. In comparison, the N. european *Porania pulvillus* loses the few actinal spines found in juveniles more quickly than the american *P. insignis.*

A fourth atlantic *Marginaster* is *M. fimbriatus* Sladen, 1889: 365–366, known only from the holotype, R 6 mm, from the Rockall Trough, W of Scotland, in 2487 metres. The name *fimbriatus* was synonymized with *Marginaster capreensis* by Ludwig (1897: 190), prompting Mortensen's inclusion of the latter in the british fauna (1927: 92). However, recent collecting in the Rockall Trough has produced several specimens from down to 2070–2210 m which are much more likely to be the same species although the smallest, R 22 mm, is much larger than Sladen's type. I believe that these are referable to the genus **Chondraster** and conspecific with *Chondraster grandis* (Verrill, 1878: 371–372), known for off Cape Cod to Cape May, U.S.A. in *c.* 400–1645 m. One of Farran's three specimens (from *Helga* st. SR 483) named by him *Culcita borealis* Süssbach & Breckner (1913: 15–16) also proved to be *grandis* besides several others from various sources extending to the Bay of Biscay at *c.* 44°N, 04·5°W. (Biogas VI st. CP 29). Arm sections and X-rays of some of them show a single horizontal row of slender tapering inferomarginal spines, as in *Porania*, numbering up to 4 on a plate, but these are completely enveloped by the very thick body wall, not individually sheathed; only by excessive shrinkage in preservation does their presence become evident externally. The proximal superomarginals are deeply inset, aligned vertical but somewhat obliquely, tall and flattened, exaggerated in form from those of *Porania*, while the inferomarginals are flattened horizontally and markedly elongated at right angles to the edge of the body, the spines usually present borne along their abradial ends (see Fig. 7D). The actinal plates are very elongated and overlap to form series linking the inferomarginals with the adambulacrals. A section of a large specimen, R *c.* 73 mm, shows only a few small, hollow, isolated abactinal plates. X-ray show the density of the other skeletal plates is also low. The adambulacral plates bear usually 2 individually-sheathed furrow spines and 2, sometimes 3, subambulacral spines within a single elongate sheath aligned almost parallel to the furrow, contrasting with the single transverse row in *Porania.* The smallest specimen, R 22 mm, from the southern Bay of Biscay, is dried, which helps to show a better developed skeleton approximating to that

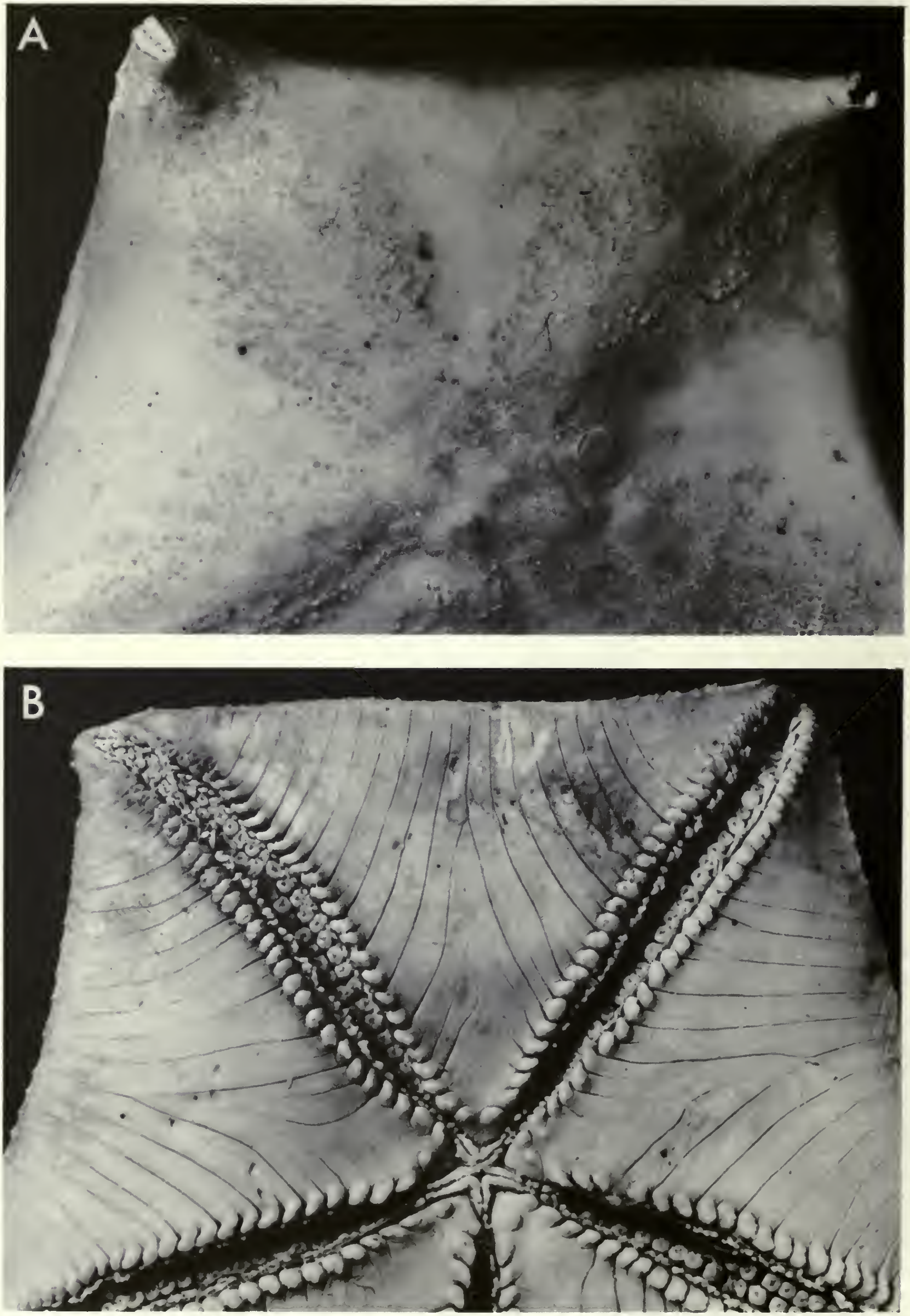


Fig. 4 A, B. *Chondraster grandis* (Verrill), 1981.7.20.1, Rockall Trough, R 73 mm; partial dorsal and ventral views. × 1½.

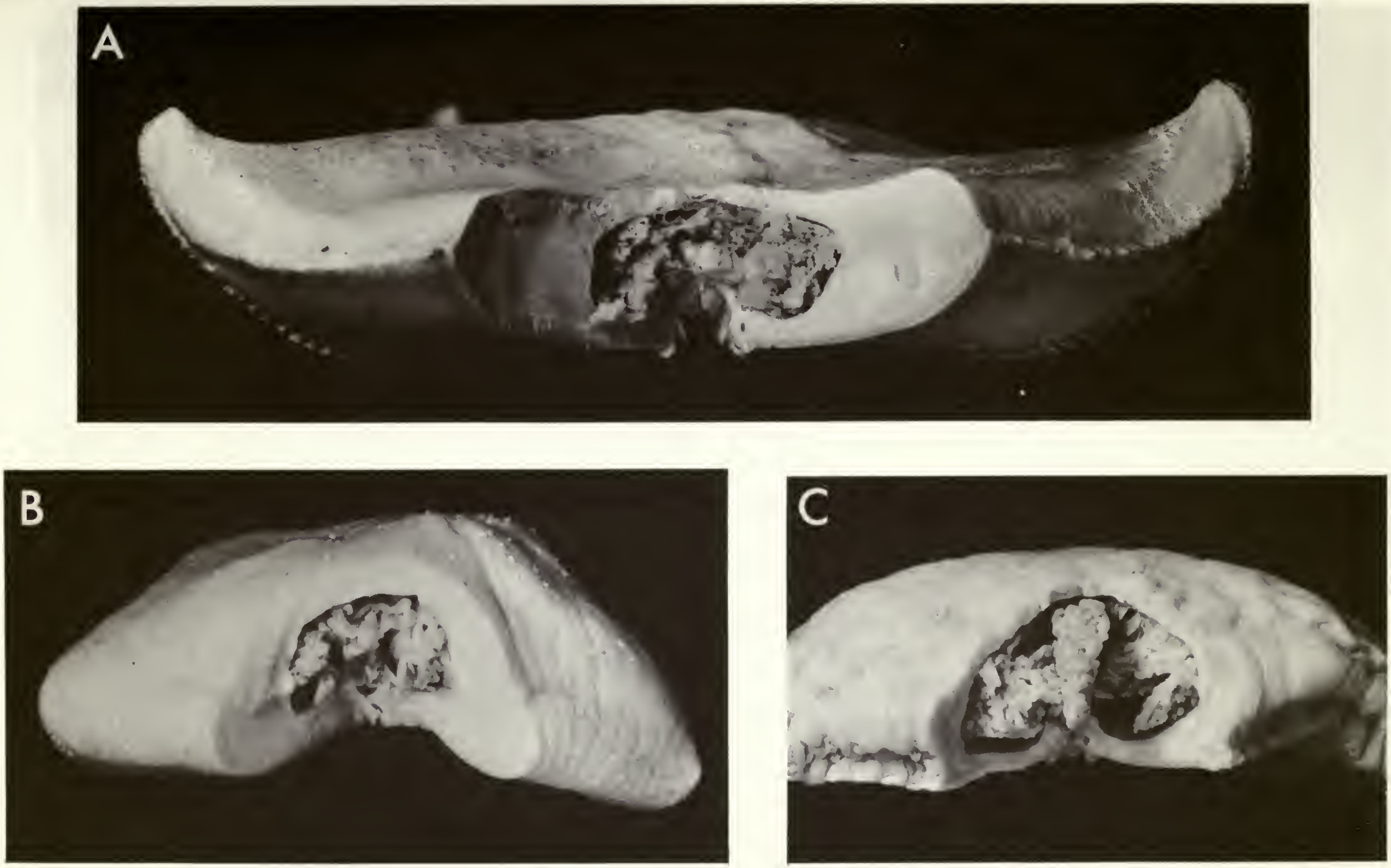


Fig. 5 Side views into the cavity left by severing an arm of: A, *Chondraster grandis* (Verrill) (as in 4A, B). B, *Porania* (*Pseudoporania*) *stormi* (Dons), 1920.12.28.31, Lousy Bank, SW of the Faeroe Is, R 40 mm. C, *P.* (*Porania*) *pulvillus* (O. F. Müller), 1974.11.25.2, Shetland Is, R 52 mm. All wet specimens, × 1½

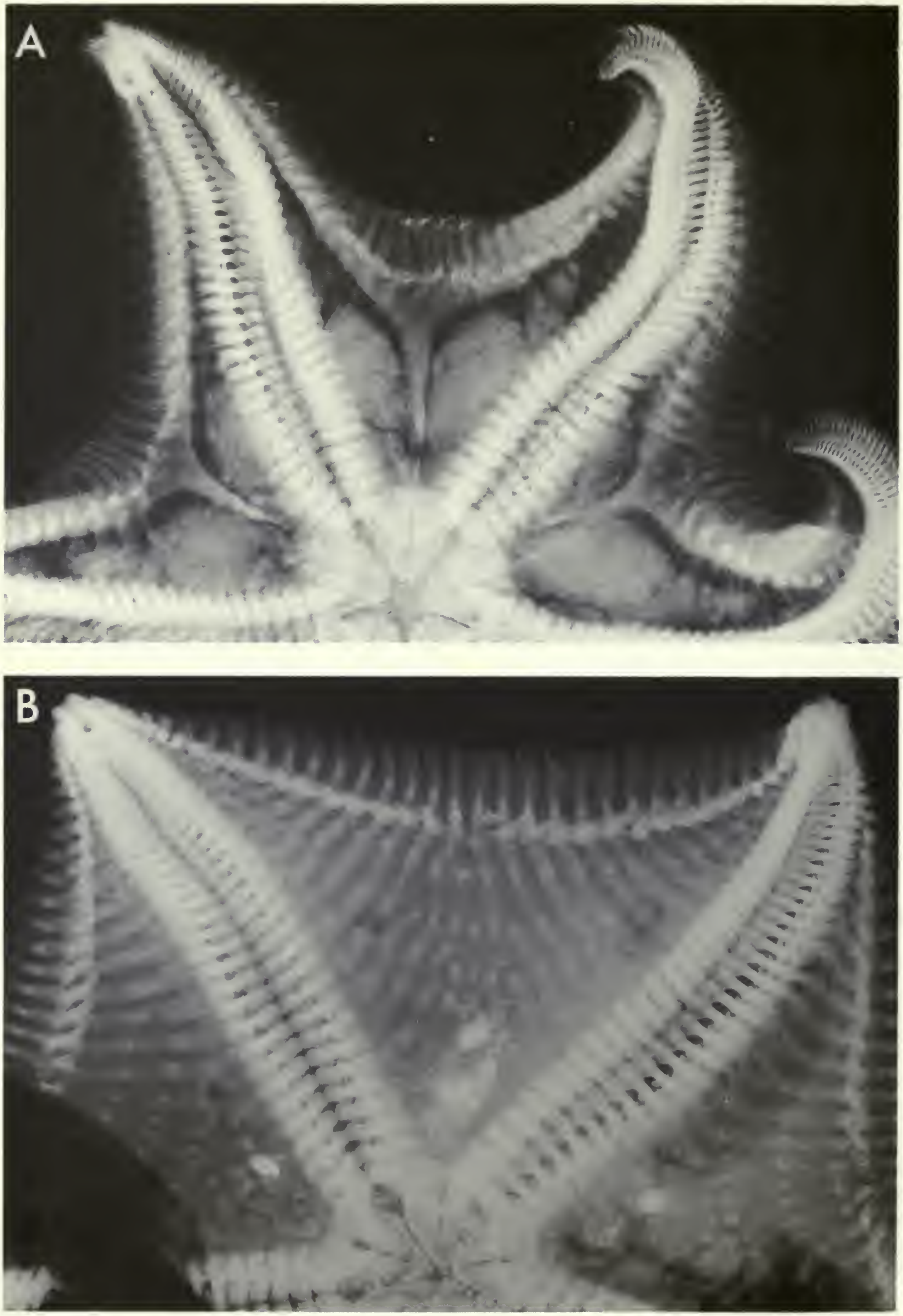


Fig. 6 X-rays of *Chondraster grandis* (Verrill): A, No details, off Cape Cod, specimen probably dried and shrunken, R *c.* 75 mm. B, (as in 4). × 1½.

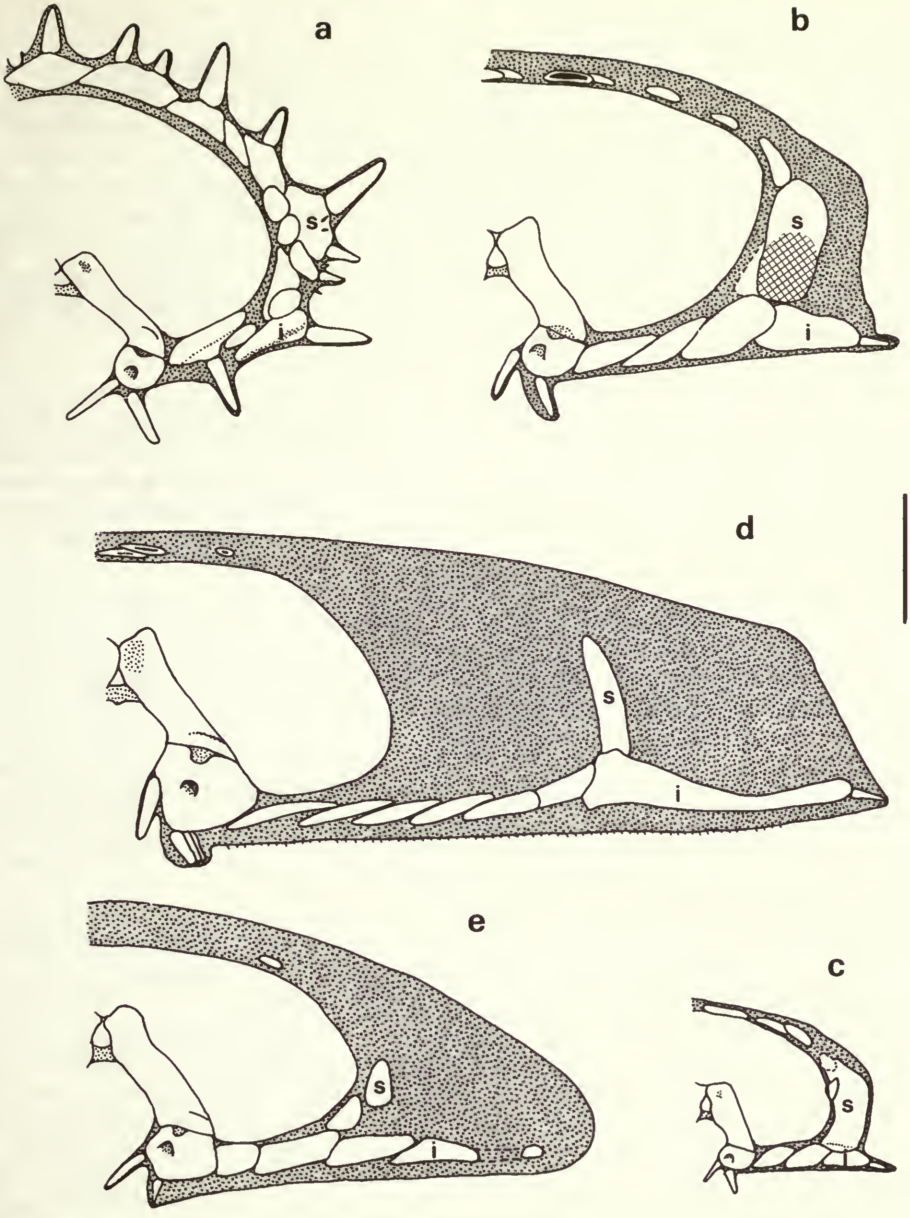


Fig. 7 Partial cross section near base of ray viewed from proximal side of: a, *Poraniopsis echinaster* Perrier, 79.8.19.6, Magellan Strait, R *c.* 37 mm; b, *Porania* (*Porania*) *pulvillus* (O. F. Müller), 1950.11.3.1, Porcupine Bank, W of Ireland, R 55 mm, the cross-hatched area of the second superomarginal hypothetical, the plate cut in sectioning; c, *P. pulvillus,* 90.5.7.511, *Porcupine* st. 8, W of Ireland, R 14 mm; d, *Chondraster grandis* (Verrill), 1981.7.20.1, *Cirolana* st. 22, E side of Rockall Trough, R *c.* 73 mm; e, *Porania* (*Pseudoporania*) *stormi* (Dons), 1920.12.28.31, Lousy Bank, SW of Faeroe Is, R 40 mm, the median part of an adjacent complete inferomarginal plate shown by discontinuous lines. i = inferomarginal, s = superomarginal. The scale measures 5 mm.

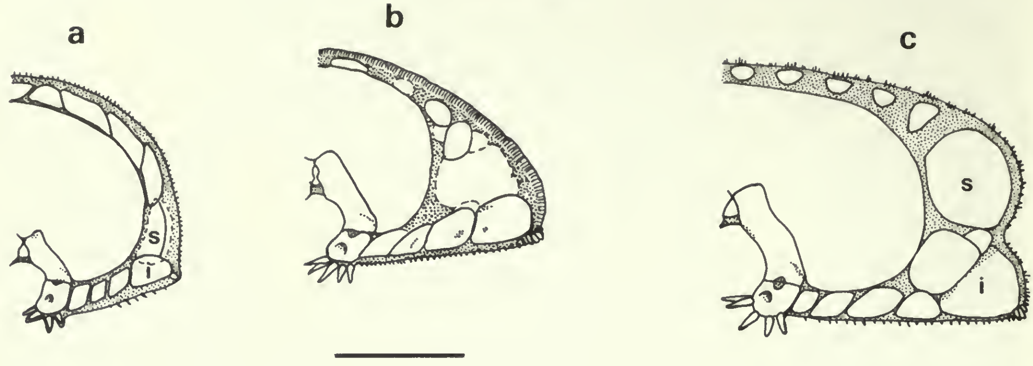


Fig. 8 Partial cross sections near base of ray viewed from proximal side of: a, *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner), IOS st. 50702, Porcupine Seabight, R 19 mm; b, *P.* (*Poraniomorpha*) *hispida* (M. Sars), 98.5.3.223, Trondheim fjord, R 26·5 mm (inferomarginal armament dubbed from another specimen); c, *P. hispida rosea* Danielssen & Koren, SMBA st. AT 230, Rockall Trough, R 33 mm. Plates well out of the plane of the section are shown by discontinuous lines; i = inferomarginal, s = superomarginal. The scale measures 5 mm.

of *Porania pulvillus* with the primary radial and interradial abactinal plates distinct on the disc and irregular carinal series linked to some of the superomarginals by transverse chains of dorsolateral plates; however, the proximal marginals are of more exaggerated form than in *Porania*. There are 2–4 inferomarginal spines on each plate and 1, sometimes 2, spines on many plates of the adjacent actinal series, as in some adults of the american *Porania insignis* and the arctic *Tylaster willei.* The larger Chondrasters all lack actinal spines and show varying degrees of skeletal reduction. The extent of the papulae is also very variable, from the two narrow bands along each ray shown in Verrill's figure (1885, fig. 44a), to a wide coverage of the upper side except for small midradial and interradial bands; some papulae may even occur between successive superomarginals.

Although these specimens are clearly conspecific with *Chondraster grandis* from the NW Atlantic, they might be subspecifically distinct. An X-ray of an american specimen, R *c.* 75 mm (Fig. 6A), shows discontinuous series of inferomarginal spines, with 1 or 2 on most interradial and some distal plates, not in between. The inferomarginals appear hollow almost to the abradial extremity in contrast to those of the NE Atlantic specimens but vestiges of actinal and possibly some abactinal plates are similarly distinguishable. Another specimen, from Lydonia Canyon, SE of Cape Cod, R *c.* 55 mm, shows up to 3 spines on most inferomarginals but no trace of any abactinal or actinal plates; the marginals themselves are ill-defined, whereas a larger similarly dried NE Atlantic individual (from Lousy Bank, SW of the Faeroes), as well as the large wet Rockall Trough specimen, show quite distinct outlines of many actinal plates at least, indicating that the dried and contracted condition is not responsible for the skeletal loss in the american specimen.

One of Verrill's two syntypes of *C. grandis* has been examined, the second is not to be found in the Peabody Museum, Yale. It is considerably shrunken and flattened with all the rays curled upwards and the distal part of one broken off. Although now in alcohol it may have dried up at some time judging from the extreme flattening and shrinkage of the body wall. Mean R is estimated at *c.* 95 mm; in life it was probably 100+ mm; r is *c.* 50 mm. Superficial spicules all over the upper side give a 'furlike' appearance; on the lower side they are more spaced out, especially proximally. The broken edge of the detached ray shows no sign of any abactinal plates, even in this distal area where resorption is likely to be minimized. However, the actinal plates are still fairly well developed, though hollow, and there are 1–3 spines on the abradial ends of four inferomarginal plates from which the tissue has been pared. Indeed, contours corresponding to actinal plates are evident all over the ventral interradii, though it does not follow that the plates remain well developed since similar contours may show in poorly preserved specimens of other skeletally deficient poraniids even though X-rays show only vestiges of actinal plates. The papulae are restricted to two narrow bands along each ray, as in Verrill's fig. 44a, 1885, and the same is true of four other american specimens, three of them from Lydonia Canyon, which is on the south side of George's Bank not far WSW from the type locality. R is *c.* 55–105 mm, probably at least 60–120 mm in life since they are dried and very shrunken so that the cluster of spinelets around the anus stands out. The number of subambulacral spines ranges from 2 or 3 in the smallest to usually 4 in the largest and the number of oral furrow spines is 6–8 with a single suboral, except in the smallest specimen which has none.

Verrill initially (1895: 138) treated *Chondraster* as a subgenus of *Porania* but in 1914 (p. 21) evidently accorded it generic rank, being followed in this by H. L. Clark (1923: 274–275) when describing a new species from South Africa. However, in 1959 (p. 160) Madsen thought subgeneric rank to be more appropriate when he described another poraniid, from E Greenland, as *Porania (Chondraster) hermanni.* Since then (pers. comm.) he has come to believe that *hermanni* is a *Porania* sensu stricto and *Chondraster* generically distinct—mainly on account of the longitudinal arrangement of the adambulacral armament in *C. grandis,* whereas *Porania* has these spines in a transverse row.

A final atlantic nominal species of *Marginaster* should be mentioned, namely *M. pentagonus* Perrier, 1882: 51) (also 1894: 165–167, pl. 11, fig. 4), the holotype and only recorded specimen of which had R 3 mm, the body form retaining post-larval flattened shape with the inferomarginal plates (numbering 6 on each side in this specimen) alone forming the periphery, the superomarginals being inset on the upper surface and resembling the somewhat imbricating polygonal abactinal plates, all bearing a scattering of spinelets. The inferomarginals each bear a comb of 6–8 spinelets along the free edge but apparently inclined downwards. On the under side most actinal plates have one or a few small spinelets and the adambulacrals bear a furrow spine and two or three subambulacral spines in a transverse series. Mortensen (1927: 94) and Tortonese (1965: 167) suggest that *pentagonus* could be conspecific with the mediterranean *M. capreensis* but that species has fewer and coarser abactinal spinelets and inferomarginal spines, judging from Ludwig's illustrations (1897, pl. 7, figs 21–23).

The type locality of *M. pentagonus* is NW of Finisterre, Spain (*c.* 44°N, 10·5°W) in 400 metres. The closest geographical record for a poraniid is that of Gallo (1937: 1664) for three specimens from Santander, N Spain, also in 400 m, resembling *Culcitopsis borealis* (Süssbach & Breckner, 1911: 217–218) although he named them *Poraniomorpha hispida* (M. Sars, 1872: 26), following Mortensen's synonymy of *borealis* with *hispida* in 1912 (p. 258) and 1927 (p. 93). The small and relatively numerous inferomarginal spinelets support inclusion of *pentagonus* in **Poraniomorpha** despite the single furrow spines which are probably correlated with the small size. However, the status of **Culcitopsis** needs reassessing since Farran (1913: 15), Koehler (1924: 160–161) and Cherbonnier & Sibuet (1973: 1348) have recorded as *C. borealis* specimens from the Porcupine Seabight (SW of Ireland) and from the NE Bay of Biscay.

Mortensen, and also Grieg (1927: 131) had discounted the swollen form and thickened body wall with reduced skeleton of *C. borealis* as insufficient to warrant more than an infraspecific difference from *Poraniomorpha hispida,* designating such specimens as forma *borealis.* Madsen too (pers. comm.) strongly supports such a low rank, believing that *borealis* is an ecophenotypic form. Certainly most poraniids show some progressive resorption of the skeleton during growth so that even in apparently well-calcified large specimens of *Porania* and *Poraniomorpha* the marginals and other plates may be hollow, as evidenced by sectioning or by X-rays—a useful technique for study of this family of thick-skinned asteroids.

In addition to the above mentioned authors, others have also commented on the considerable variation in several directions of *Poraniomorpha hispida,* notably Djakonov (1946: 163–169, at length, in russian), who compared it with the exclusively arctic *P. tumida*

(Stuxberg, 1878: 31), finding intermediate specimens where the ranges of the two overlap (presumably in N Norway and the Barents Sea), mentioning this briefly in his book on russian asteroids (1950: 59, translation 1968: 50). Unfortunately it is not possible to ascertain the adult form of Sars' material since his holotype (from the Lofoten Is, N Norway, 365–550 m) has R only 6 mm. Although it does have a near pentagonal form, R/r 1·2/1 (see Sars, 1877, pl. 8, figs 24–26), this could be true of a more stellate adult when young. However, Grieg (1927: 129–133) makes several references to the 'typical' form, which by implication is a shorter-rayed one since he also refers separately to forma *rosea,* Danielssen & Koren's holotype of which had R/r 1·67/1 and appears relatively stellate in their figures. Djakonov (1950) also described *P. hispida* as having a massive body, broad disc and broad, very short, rays. In the absence of any evidence to the contrary, this is the form which can be attributed to 'typical' *hispida.* All nine norwegian specimens in the British Museum collections with well developed skeletons (from Hardanger and Trondheim fjords, from SW of Bergen and off the North Cape) consistently have a pentagonal form, R/r 1·3–1·5/1 (R 7–45 mm). Östergren (1904: 615) recognized *rosea* as a distinct variety of *hispida*, followed by Grieg (1907: 42) who noted that specimens from Bergen and Trondheim fjords as well as from Bohuslan in the vicinity of Oslo fjord (i.e. close to shore) are short-rayed whereas those from the deep area of the Skagerrak (500–600 metres) have relatively long rays. The latter form with R/r *c.* 2/1 and triangular rays forming angular interradial arcs was illustrated by Mortensen (1927, fig. 53, taken from his earlier 'Danmarks fauna') but does not appear to be found on the continental shelf in british waters, only from the bathyal at 900–1400 metres to the NW and W of the British Isles, from which *c.* 20 specimens are consistently stellate. These include two small syntypes of *Lasiaster villosus* Sladen, 1889: 372 (synonymized with *Poraniomorpha hispida* by Grieg and others), the specimen from *Helga* st. SR 506 (Fig. 11 B, C) named *P. villosa* by Farran (1913: 17) and others more recently collected in the Rockall Trough and Porcupine Seabight. The only exception is the holotype of *Rhegaster murrayi* Sladen, 1889: 368–371 (Fig. 11 D, E) (another synonym of *P. hispida*) from the Wyville Thomson Ridge in 510–790 metres, which has a near pentagonal form, R/r 1·3/1 but R only *c.* 14 mm. The type locality of *Poraniomorpha rosea* Danielssen & Koren, 1881: 189–192; also 1884: 67–70, the oldest species-group name for stellate european specimens, is NW of Bergen (61°41′N, 03°19′E) in 402 metres, that is in the southern arm of the Norwegian Sea which leads to the Skagerrak. On the basis of this evidence, it is possible that short and long rayed specimens are isolated in different water masses. However, Madsen (pers. comm.) finds considerable overlap in norwegian waters. Nevertheless I believe that *rosea* can be accorded at least subspecific rank.

It should be noted that *rosea* is antedated by two other names long synonymized with *P. hispida,* namely *Asterina borealis* Verrill, 1878: 213–214 and *Porania spinulosa* Verrill, 1880a: 202–203 (Fig. 11F), based on moderately long-armed type material from american waters N and E of Cape Cod. R/r of the respective types is 12/7 = 1·7/1 (implying a higher value when fully-grown) and 40/23 = 1·75/1. Paucity of american material for comparison prevents a proper assessment of the affinites of specimens from east and west and I can only note that the american ones appear to have the interradial arcs more curved and the tips of the rays blunter than is usual in european ones. In 1895 (p. 139) Verrill noted that *spinulosa* was taken 'mostly in the warm area' and *borealis* in the 'cold area' but in 1880 (b: 401) he had recorded both from USFC stations 869 and 879 and in 1914 (p. 18) he remarked that his 1895 notes (p. 139) on a relatively large specimen (R/r 35/23 mm) from the Fishing Banks (*c.* 45·5°N, 57°W, in 170 fathoms) refer not to *borealis* but to *spinulosa.* With such confusion and overlap it is impossible to assess if two infraspecific taxa exist in american waters until more material is available.

With regard to the decalcified adult specimens such as have been referred to *Culcitopsis borealis* (Süssbach & Breckner), the range of these appears to parallel to a great extent that of *P. hispida rosea.* Twelve samples range from the Porcupine Seabight W of southern Ireland N and E to the Faeroe Channel, Shetlands and N Norway (Lofoten Is) in depths down to *c.* 1000 metres though with a minimum of only 110 metres. These show a near-

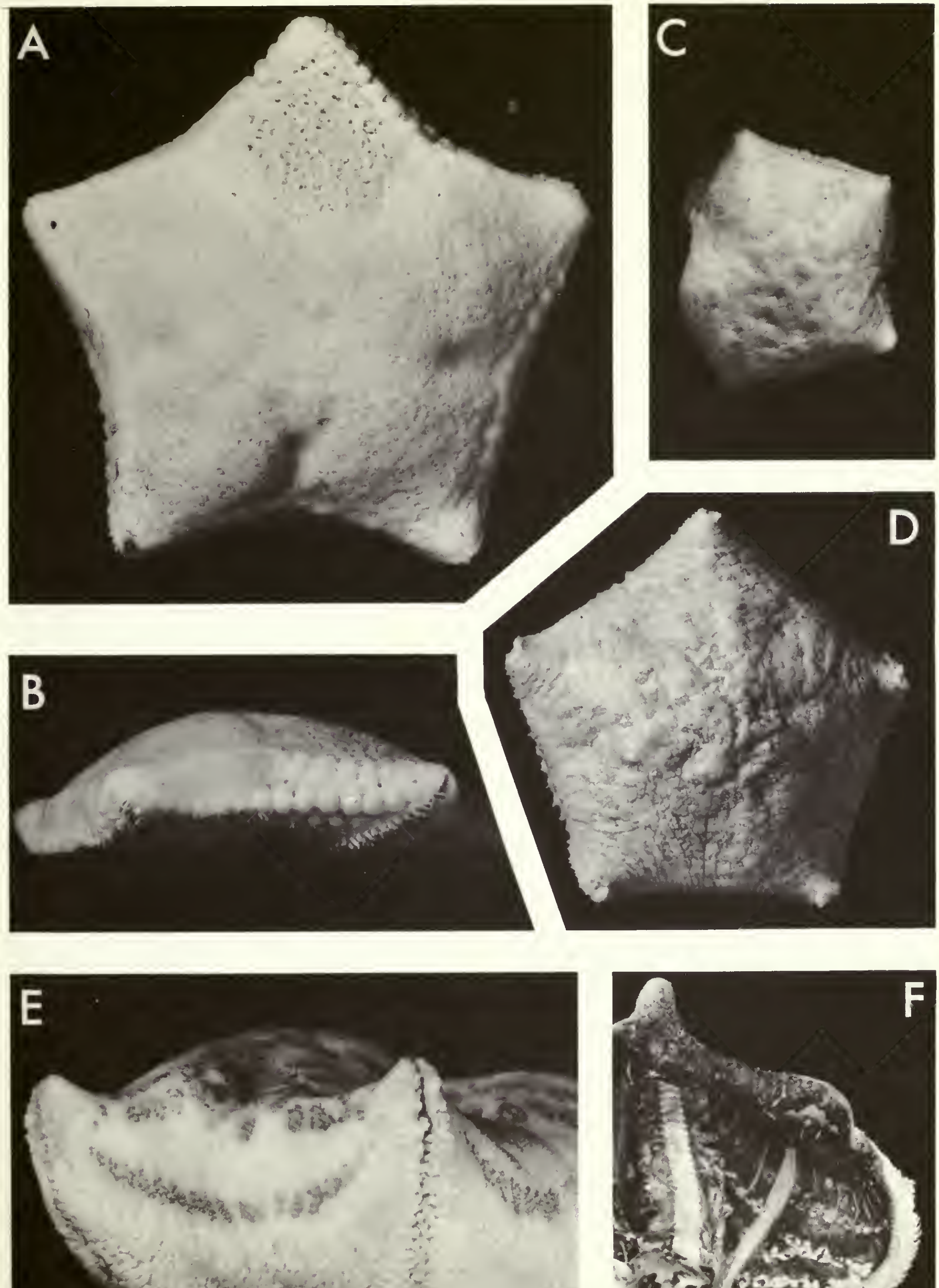


Fig. 9 A, B, *Poraniomorpha* (*Poraniomorpha*) *hispida* (M. Sars), 91.4.15.1, Trondheim fjord, R 32 mm, dorsal and side views, partly denuded. C-F, *P.* (*Culcitopsis*) *borealis* (Süssbach & Breckner): C, (as in 8a); D, 1956.5.25.5, E of Shetlands, R 25 mm, both dorsal views; E, F, 1974.1.4.2, E of Wyville Thompson Ridge, R *c.* 44 mm, side views, E wet, external; F dry, internal. Others all wet, × $1\frac{1}{2}$.

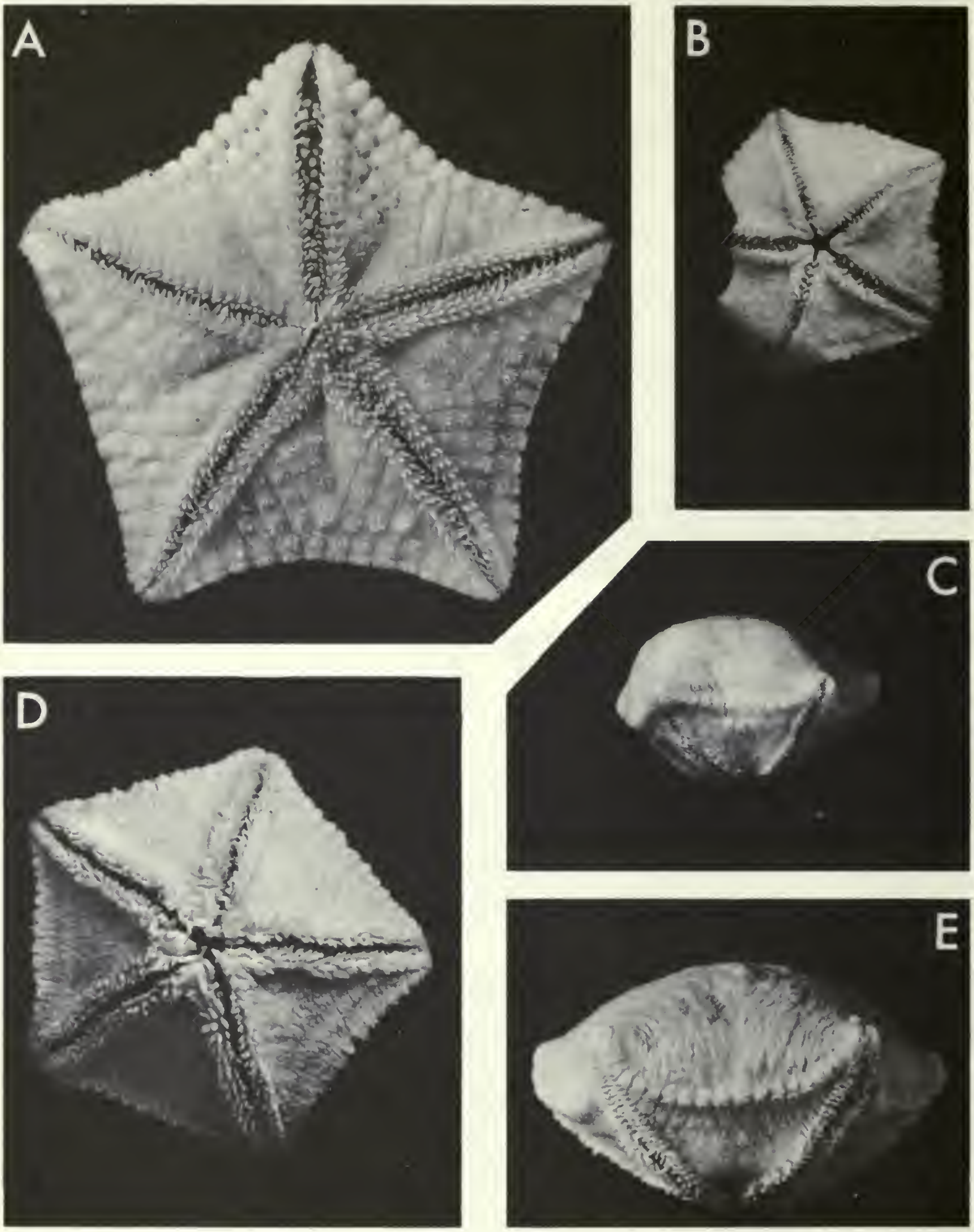
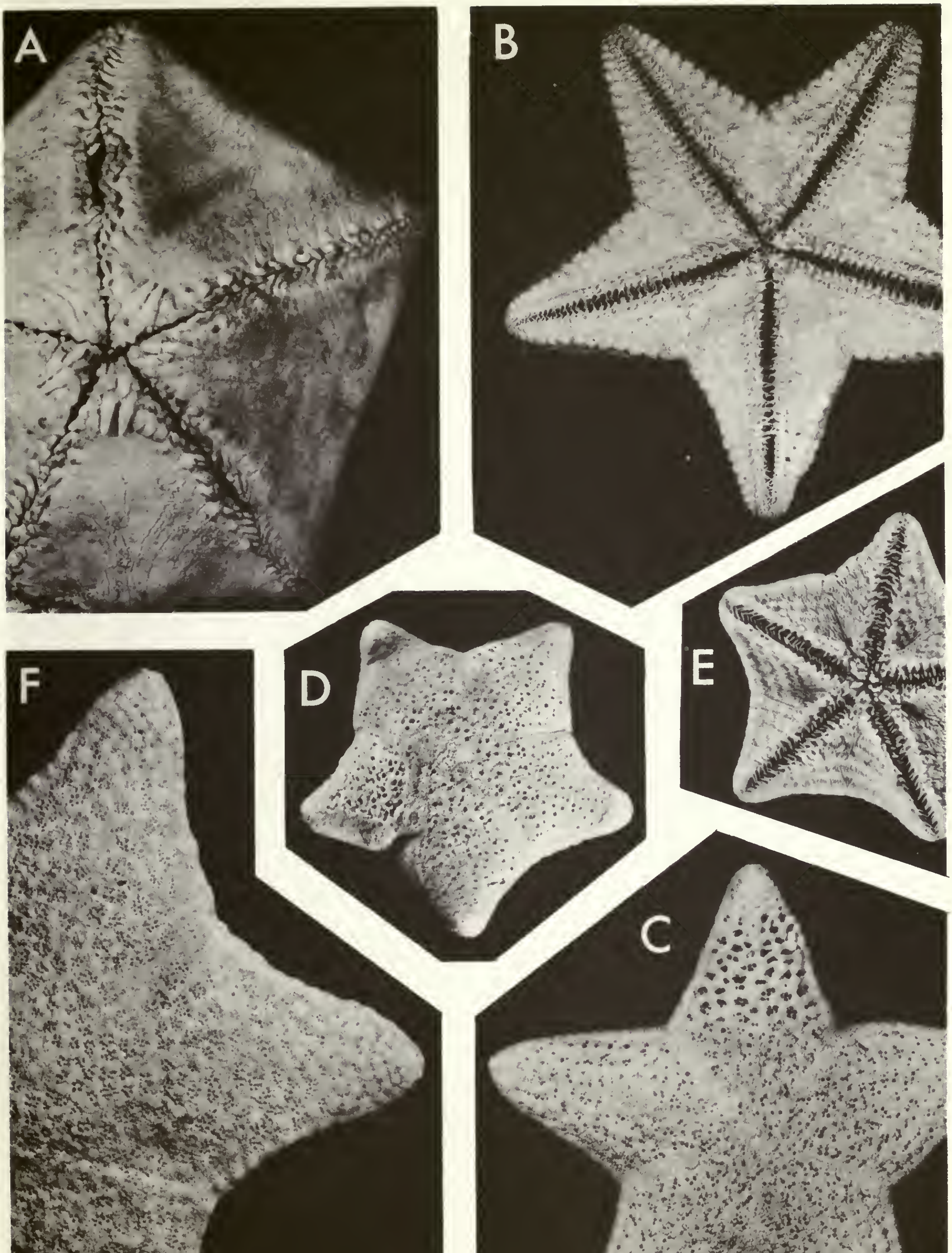


Fig. 10 A, *Poraniomorpha* (*Poraniomorpha*) *hispida* (M. Sars) (as in 9A, B), ventral view. B–F, *P.* (*Culcitopsis*) *borealis* (Süssbach & Breckner): B, C, (as in 8a) ventral and side views; D, E, (as in 9D) ventral and side views. All wet, × 1½.

Fig. 11 A, *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner), National Museum of Ireland no. 102.1913, *Helga* st. SR 223, R *c.* 40 mm, ventral view. B,C, *P.* (*Poraniomorpha*) *hispida rosea* Danielssen & Koren, Nat. Mus. Ireland 403.1913, *Helga* st. SR 506, R 28 mm, ventral and dorsal views. D-F, *P. hispida hispida* (?): D, E, holotype of *Rhegaster murrayi* Sladen, 90.5.7.545, *Triton* st. 5, Wyville Thomson Ridge, R *c.* 14 mm, dorsal and ventral views; F, presumed holotype of *Porania spinulosa* Verrill, Peabody Museum, Yale no. 9867, off Cape Cod Light, R 40 mm. A, wet; others dry; D, E × 2; others × 1½.


A
B
D
E
F
C

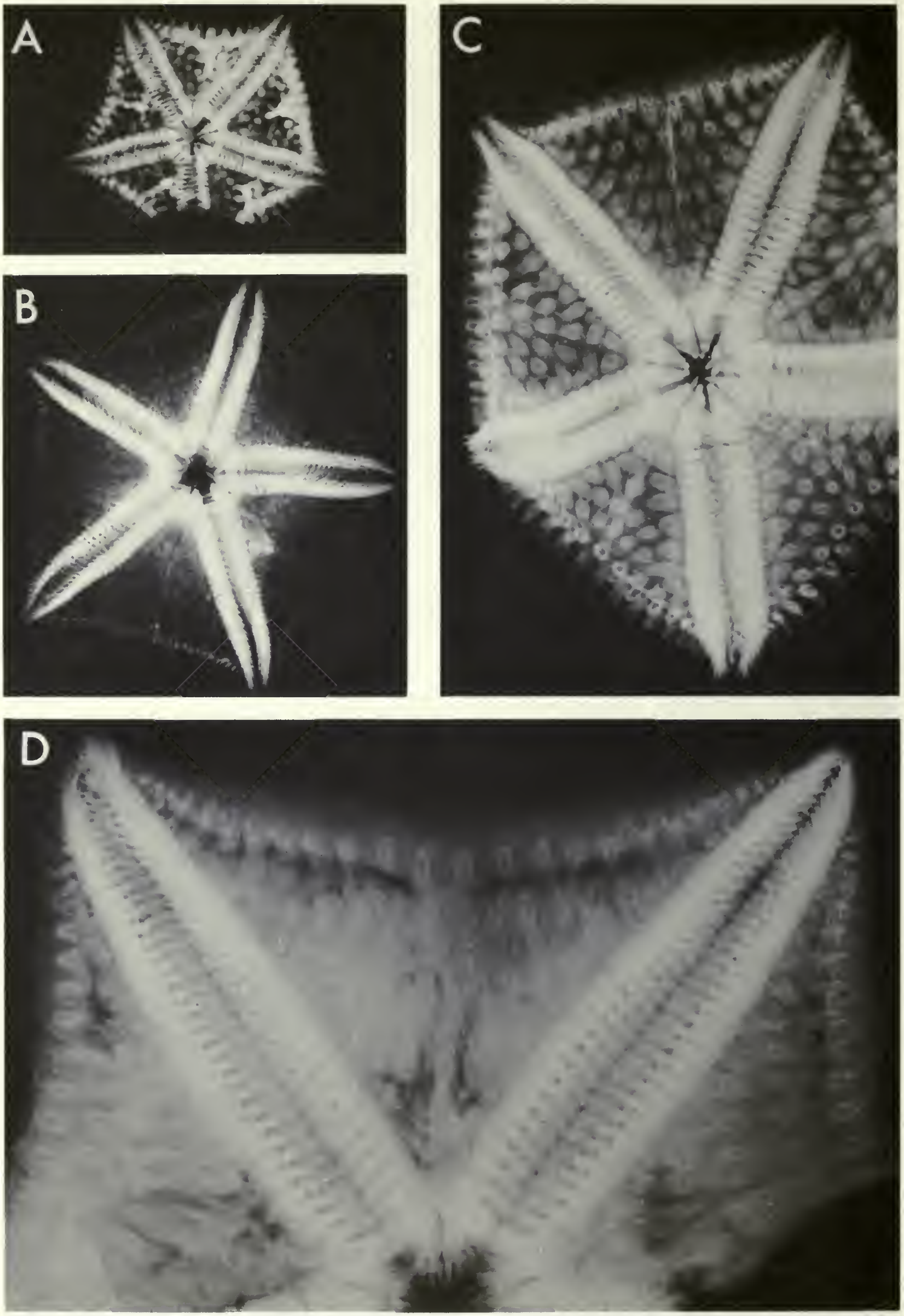


Fig. 12 X-rays of *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner): A (as in 8a); B (as in 9D); C, IOS st. 50601, Porcupine Seabight, R 35 mm; D, 1965.5.24.4, Lofoten Is, R. *c* 72 mm. × 1½.

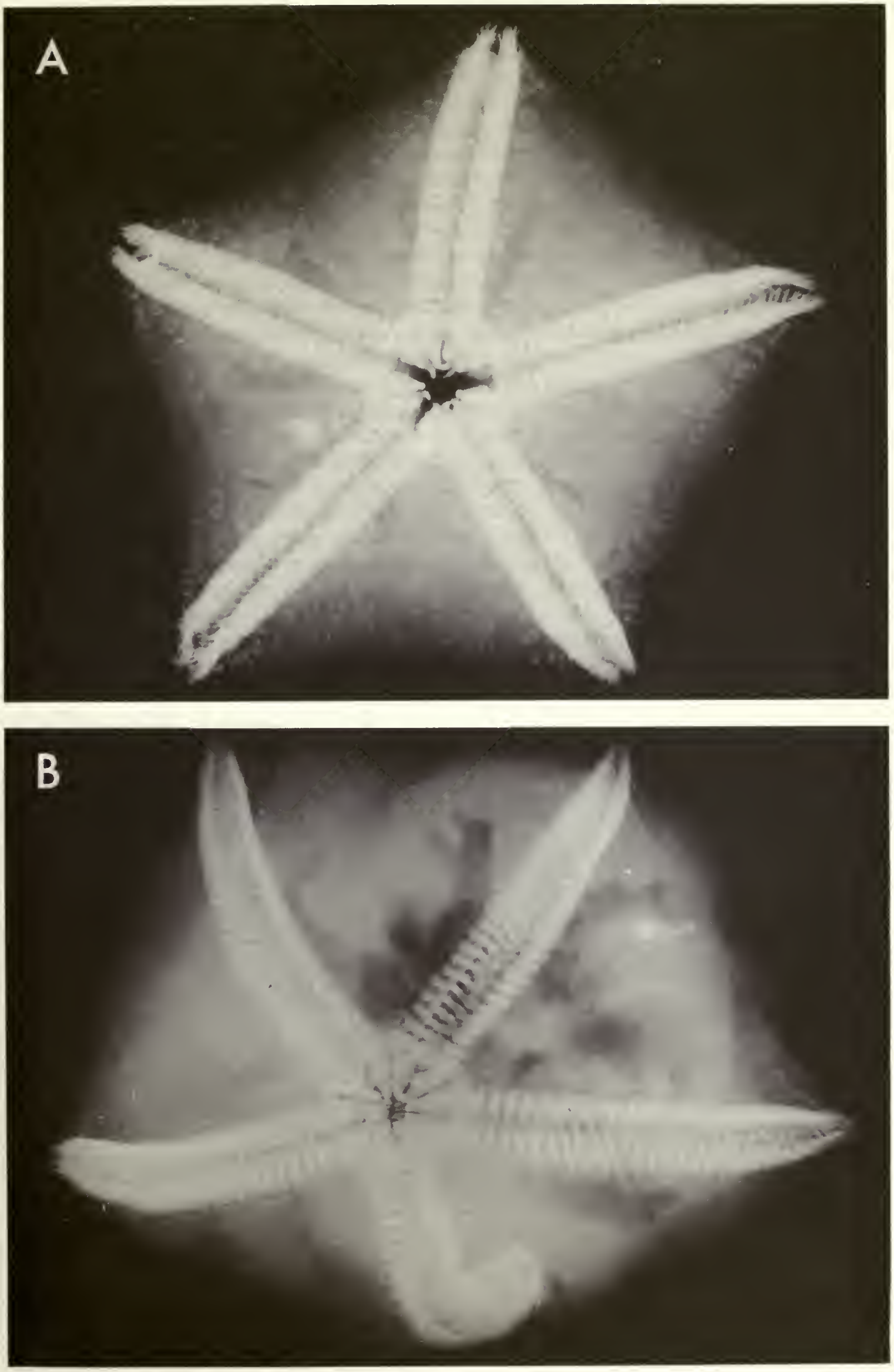


Fig. 13 X-rays of *Poraniomorpha* (*Culcitopsis*) *borealis* (Süssbach & Breckner): A, IOS st. 9752, Porcupine Seabight, R 40 mm; B, 1966.1.13.45, SE of Wyville Thomson Ridge, R. *c.* 47 mm. × 1½.

pentagonal outline, R/r < 1·5/1, are more or less high and cushionlike with the body wall thickened and agree with Süssbach & Breckner's holotype of *C. borealis*, taken NE of the Shetlands in 134–215 metres. The papulae are in close clusters, the upper surface otherwise appearing fairly smooth superficially but studded with numerous embedded fine spinules visible under magnification, the ventral surface somewhat pustular and the adambulacral spines heavily sheathed. Most of these characters are at variance with 'typical' *Poraniomorpha hispida* where the body is flattened though thick and the superficial armament is distinct and almost continuous, covered over with only thin skin.

X-rays of six of the *borealis*-like specimens ranging in size from R 19–72 mm are shown in Figs 12 and 13. As would be expected, the maximum calcification of the skeleton appears in the smallest where the interbrachial septa are partly calcified. However, even here many of the marginals and actinals (or abactinals) showing in the interradii have a fairly large central cavity and the body shape (Fig. 10C) is markedly inflated, much as in Greig's specimen of similar size (1927: 132–133, figs 3–5) from *Michael Sars* st. 32 (W of Kristiansund, Norway, 400 metres, upon which (rather than his larger ones) I suspect Grieg based his observation that 'the skeleton of the disc is well developed and agrees completely with that of *Poraniomorpha hispida'* though he notes that the surface armament is hidden in the thick skin. Although the rate of calcite resorption varies to some extent as shown in the X-rays (compare Figs 12C & 13 A, B), at R>40 mm only vestigial outlines of most plates are evident, at best. This compares with a flattened Trondheim specimen of *P. hispida* (Figs 9A, B, 10A, 14) with R *c.* 32 mm in which the abactinal and actinal plates and interbrachial septa appear well calcified and the marginals solid and blocklike. Even in a specimen of *hispida* with R>50 mm, from the Skagerrak in 660 metres, X-ray kindly sent by Dr Madsen, the skeletal development still appears much the same except that the interradial plates of one of the marginal series are reduced and hollowed to a similar extent as the corresponding plates of the *borealis* with R only 19 mm (Fig. 12A). Clearly there should be considerable similarity in the skeletons of juvenile *borealis* and *hispida*, the main skeletal differences

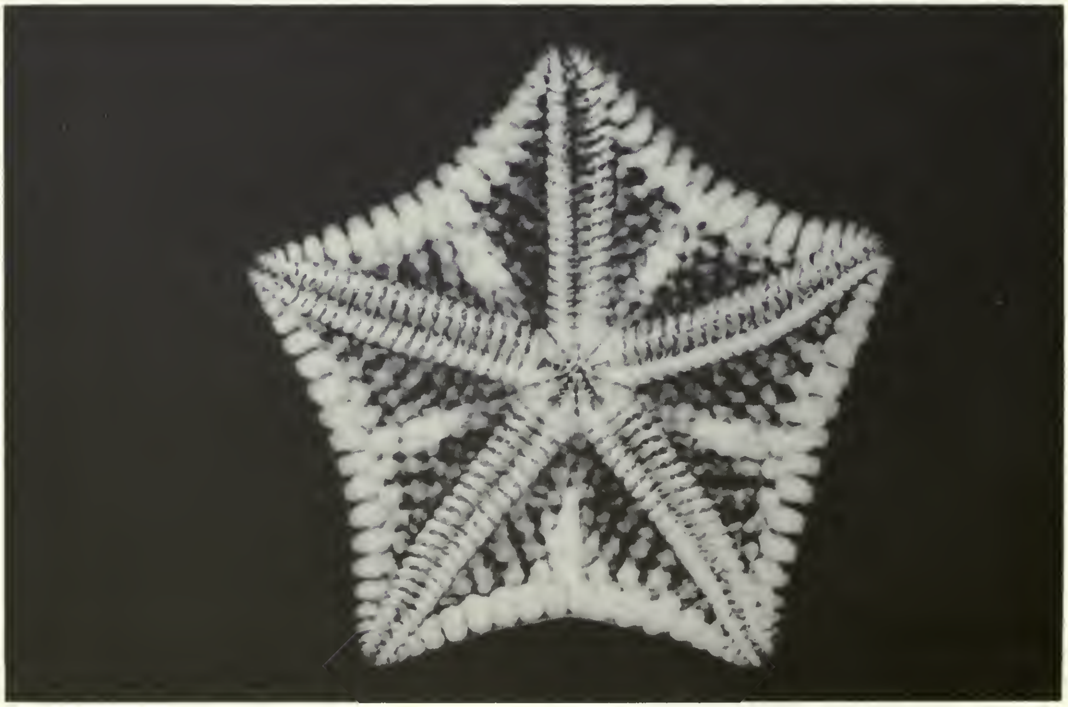


Fig. 14 X-ray of *Poraniomorpha* (*Poraniomorpha*) *hispida* (M. Sars) (as in 9A, B). ×1½.

being in the timing and extent of resorption. However, the resultant morphological difference in well-grown specimens is so marked (compare also the side views shown in Fig. 9B, E) that I find it impossible to believe there is insufficient genetic difference to justify a specific distinction for *borealis,* as well as a subgeneric one for *Culcitopsis* within the genus *Poraniomorpha.* My conclusion that *borealis* is more than just a form of *hispida* is supported by a notable enlargement and distal inclination of a single pair of suboral spines on each jaw of most specimens of *borealis* (see Fig. 11A), suggesting a modification in feeding habits (perhaps approaching that of *Odontaster* which has similar projecting but hyaline-tipped oral spines used for rasping on sponges). A similar modification, but of the apical pair of oral spines, is shared by *Poraniomorpha bidens* Mortensen, 1932: 9–12 from Greenland (recently taken also in the cold area of the Faeroe Channel NE of the Wyville Thomson Ridge). *P. bidens* has a furlike coating of very fine superficial spinules of papillae clearly visible through the thin skin, as in *P. hispida,* but a general body form with tapering pointed rays, as in the other arctic species, *P. tumida* (Stuxberg) where the superficial armament is much coarser, almost granuliform. Additionally, the colour in life of *borealis* appears to be generally much paler than that of *hispida,* the darkest cited being pale orange above; it is more often yellow or pale yellow, white below, whereas *hispida* is said to be: rose red above, orange below; dark violet-red above with white papulae, reddish-white below, or pale reddish-yellow all over.

As mentioned previously (p. 34), intermediates exist in northern Norway between the polymorphic *hispida* and *tumida* where the two taxa overlap. Clearly the taxonomy of the entire genus *Poraniomorpha* needs to be reviewed, not just the Atlantic members within the scope of the present study.

It should be noted that in addition to the natural differences correlated with the skeletal development, decalcified specimens can be drastically modified in appearance by changes in preservation. For instance, the large specimen, R 72 mm (Fig. 12D) from the Lofoten Is in the British Museum collection, thought to be *P. (C.) borealis* is badly flattened with the upper side crinkled and the whole body wall excessively contracted so that the superficial spinules are brought together in an almost continuous coating, as is usual in *Poraniomorpha hispida,* the identification it had prior to being X-rayed. The extent of shrinkage possible in these poraniids is shown by the holotype of *Sphaeriaster berthae* (Dons, 1938: 163–164), from N of the Lofoten Is, which had R 90–115 mm in life but was only 77–80 mm after preservation in spirit. Change in body shape may also be drastic, as shown by *Spoladaster veneris* (Perrier), from St. Paul's I, southern Indian Ocean where live specimens may be markedly stellate but preserved ones become pentagonal—see A.M.C., 1976, pl. 6 and pl. 3, fig. 2. Madsen and I have no doubt that *S. berthae* is synonymous with *borealis* so that **Sphaeriaster** itself is a synonym of *Poraniomorpha.* Dons's second nominal species, *S. bjoerlykkei,* (1938: 165–168) type locality N of the Shetlands in 300–350 metres, R/r 87/47 = 1·7/1 so fairly stellate, shows a high density of superficial spinules as in our Lofoten Is specimen just mentioned. A new X-ray sent by Madsen shows very faint outlines of plates, much as in large *borealis*, but he thinks that it is more likely to be decalcified *P. tumida*; Dons described multiple furrow and subambulacral spines, more than usual in *borealis.*

Another taxon with a very reduced skeleton in larger specimens is **Spoladaster** Fisher. In 1976 (in Clark & Courtman-Stock: 73) I suggested that *Tylaster meridionalis* Mortensen, 1933: 249–250, from the same area W of South Africa, based on a specimen with R only 28 mm, is probably a synonym of *S. brachyactis* (H. L. Clark, 1923: 293–294), of which R is 40–80 mm in the few specimens recorded. Studies now on the growth changes and variation of *P. (C.) borealis* confirm me in this view. It is noteworthy that no better-calcified Poraniomorphas have been collected in south african waters. *S. brachyactis* shows some development of macroscopic inferomarginal and actinal spines, such as are found in greater numbers in *Tylaster willei* Danielssen & Koren, 1881: 186, from the northern Norwegian Sea (see Danielssen & Koren, 1884: 64–67). This species too has the underlying skeleton very reduced. These taxa illustrate the ability of poraniids to utilize coarse armament even though this is, at best, articulated only to rudiments of skeletal plates in the thickened body wall. **Tylaster** and the other arctic taxa mentioned come within the range of the series 'Marine Invertebrates of Scandinavia', the asteroid part of which is in preparation by Madsen. Hopefully he will be able to clarify the relationships of these if more material is available.

There is yet one more conspicuous example of skeletal reduction in poraniids, exemplified by **Pseudoporania** Dons. Again I am indebted to Madsen for an X-ray, of the holotype of *P. stormi* Dons, 1936: 17–20, from Trondheim fjord in 300 metres, R 83–96 mm. This shows that the actinal and marginal plates have contracted down into very small, widely separated rods or partially hollow nodules of calcite, the more interradial inferomarginals being apparently reduced to a rudiment of their abradial, possibly also adradial ends. This is just the progression I would expect from the condition found in six much smaller specimens, R 19–40 mm, one from the Porcupine Seabight, the others from around the Wyville Thomson Ridge, S of the Faeroes, in depths of 360 (?183)–770 (?927) metres. These too have a smooth surface above and below, apart from well-marked actinal grooving. Sectioning shows the lateral body wall to be extremely thick (Fig. 5B) and X-rays show no signs of inferomarginal spines, even on the distal plates in the smallest (Fig. 16A, B), the ambitus being rounded. The body form is flattened and pentagonal whereas Don's specimen has short tapering rays. The papulae are relatively sparse and scattered. The adambulacral plates are armed with single furrow and subambulacral spines (the sheath of the latter continuous with the thickened ventral body wall), which appeared to provide a distinction from *stormi* but Madsen informs me that it too has single spines, Dons' description of 2+2 being incorrect. The smallest specimen has the marginals blocklike except for the interradial inferomarginals which project abradially. The sections and X-rays show progressive attenuation of the plates with division of the interradial inferomarginals into two small end pieces, ad- and abradial, by loss of the middle part. This is very different from the resorption shown by *Poraniomorpha (C.) borealis*, which is almost entirely from the inside, the plates being reduced to hollow, usually rectangular or ovate, shells. The complete absence of any superficial spinules and the small number of adambulacral spines, with only single furrow spines, agrees more closely with **Porania** than any other genus of the family, though the great thickening of the body wall and the absence of a distinct ventrolateral angle emphasized by a horizontal fringe of individually sheathed inferomarginal spines results in a very different appearance.

In 1983 (*in* Gage et al.: 281) I noted that a specimen of *Porania pulvillus* (O. F. Müller, 1776: 234) from the Rockall Bank in 148 metres with R 55 mm has the inferomarginal spines drastically reduced from the usual 3–5 on each plate to only 1 or 2 on some of the more interradial plates and none on the distal plates. Nevertheless, the remaining spines are individually sheathed and projecting from the ambitus and the usual ventrolateral angle is still distinct, the body wall not being markedly thickened. An X-ray of this specimen (Fig. 18B) shows that a few of the interradial inferomarginal plates are slightly compressed, recalling those of the smallest specimen of *stormi* (Fig. 16A), though the modification is much less. Madsen (pers. comm.) has found occasional specimens of *P. pulvillus* from Norway with the inferomarginal spines more or less reduced but the skeleton otherwise well developed. Additionally he has sent X-rays of two other specimens, R probably 25–30 mm, with the interradial marginals much reduced, some divided into two parts and the body wall obviously much thickened. Although he finds these akin to *Pseudoporania stormi,* he considers this to be a synonym of *Porania pulvillus.* One (from S of Iceland, *Thor* st. 166) appears to have nearly all the marginals narrowed down and completely lacking spines, much as in the Porcupine Seabight specimen (Fig. 16B) but the other (Tromsø Museum, probably from N Norway) has about 3 inferomarginal plates each side of the very reduced interradial plates in each interbrachial arc with a rhombic abradial part bearing 1, rarely 2, large spatulate spines.

In face of such intermediate specimens, there can be little doubt that *Pseudoporania* should be referred to the synonymy of *Porania,* in a comparable way to *Culcitopsis* and *Poraniomorpha.* However, the general form of adults of the several *Porania* species, with a distinct ventrolateral angle and the body wall no more than moderately thickened is so

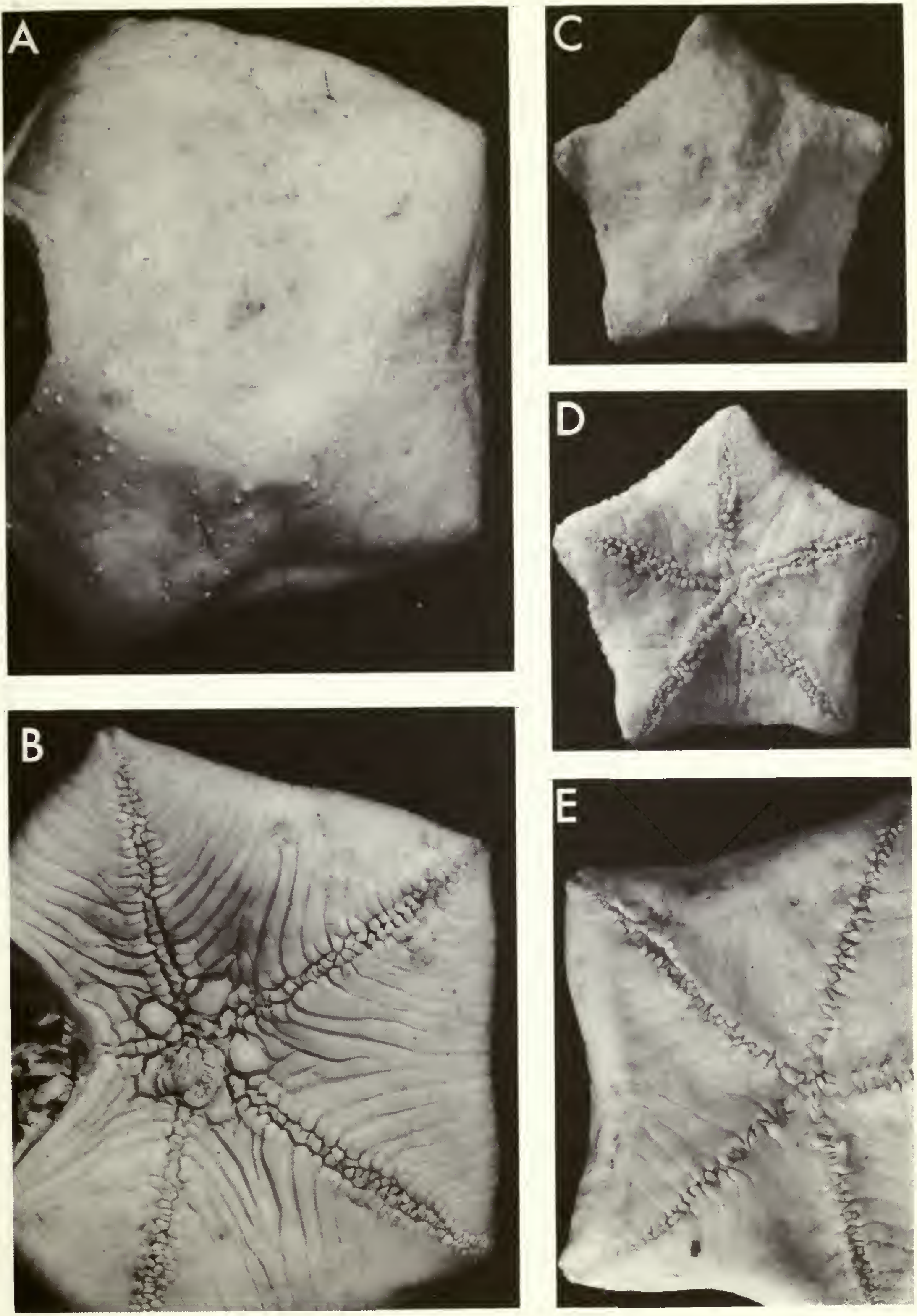


Fig. 15 *Porania* (*Pseudoporania*) *stormi* (Dons): A, B, (as in 5B), dorsal and ventral views; C, D. Royal Scottish Museum, *Walter Herwig* st. 848, S of Faeroe Is, R 19 mm, dorsal and ventral views; E, IOS st. 50601, Porcupine Seabight, R 35 mm. All wet, × 1½.

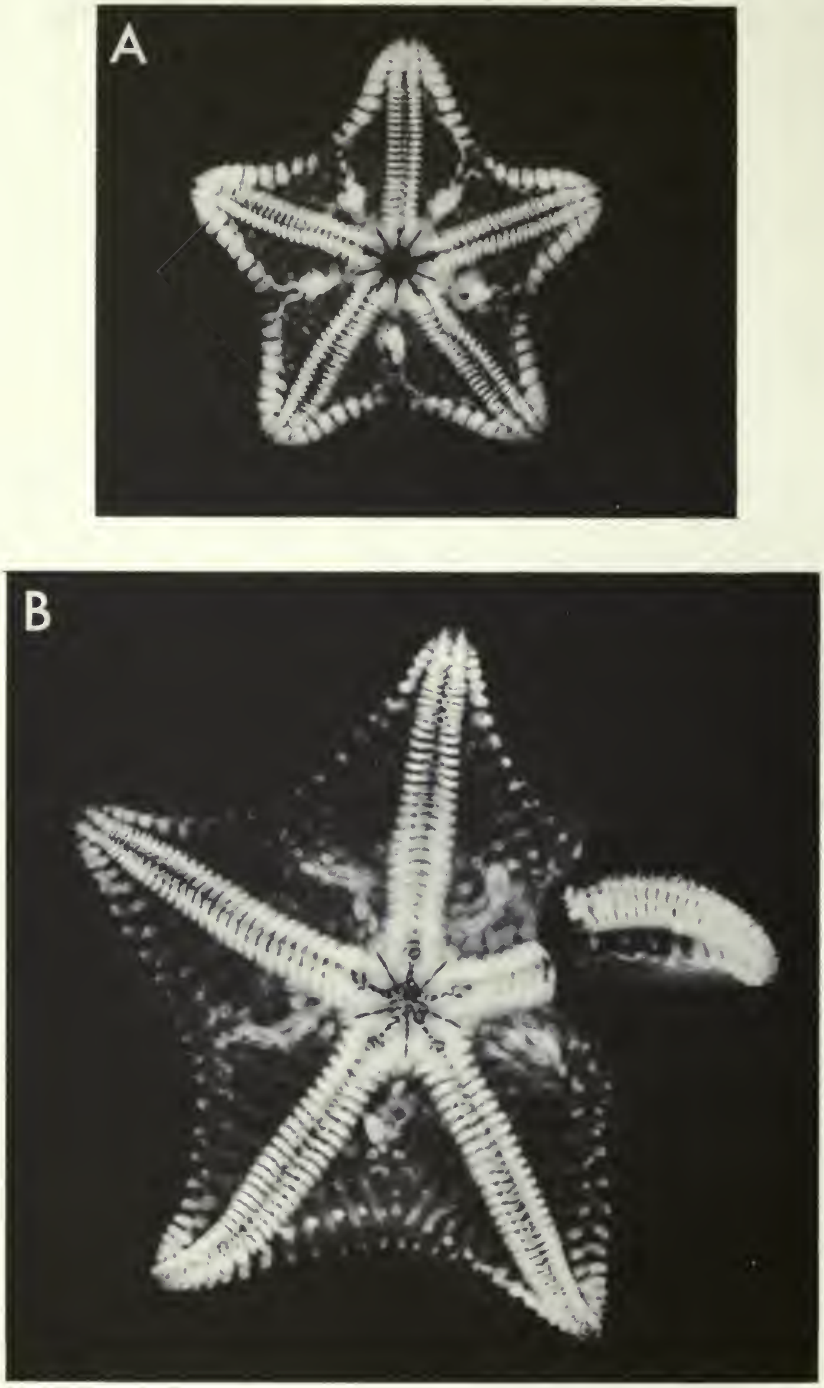


Fig. 16 X-rays of *Porania* (*Pseudoporania*) *stormi* (Dons): A (as in 15B, C); B (as in 15E). × 1½.

consistent that here again I believe a subgeneric distinction is justified, in spite of Madsen's opinion to the contrary. It seems likely that *P. stormi* is zoogeographically isolated from *pulvillus*. The present records indicate that *pulvillus* alone is found on the shelf around the British Isles and in southern Norway N to about Trondheim fjord, to a minimum depth of

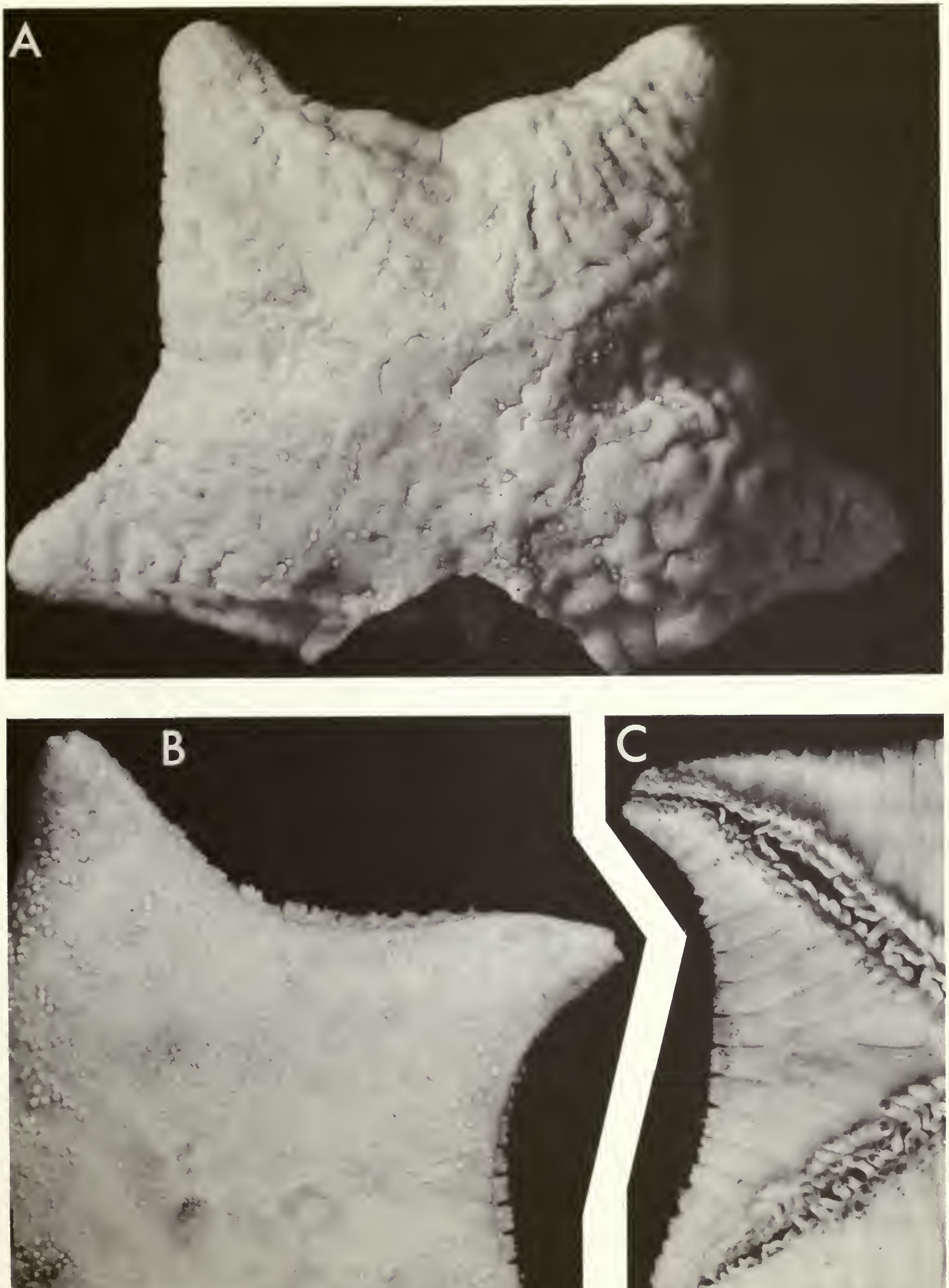
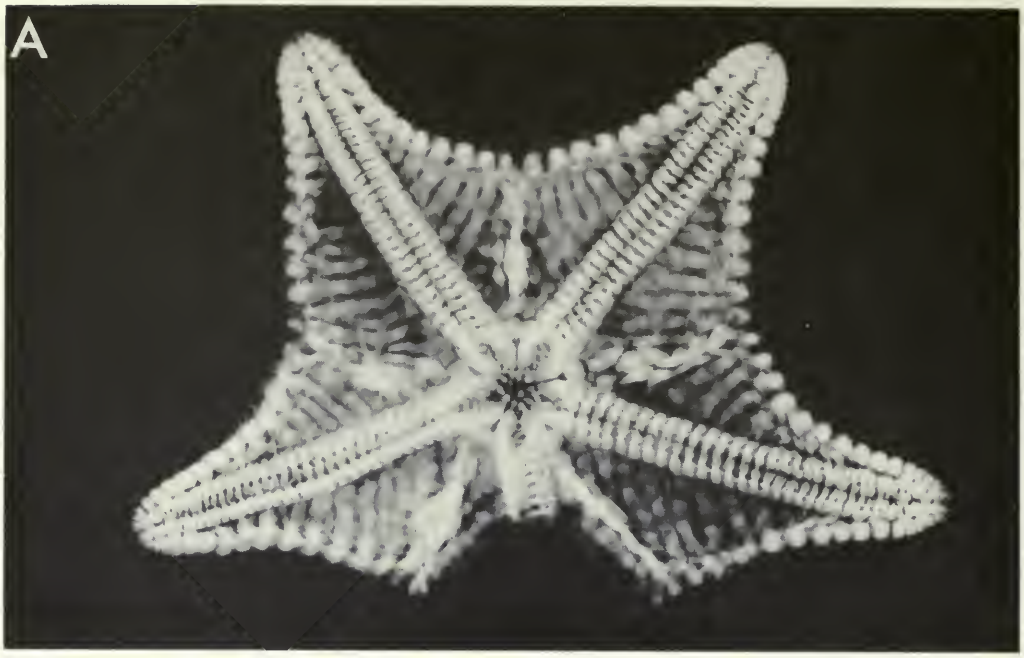


Fig. 17 *Porania (Porania) pulvillus* (O. F. Müller): A (as in 5C); B, C, 1950.11.3. 1, Porcupine Bank, R 55 mm, dorsal and part ventral views. Both wet, × 1½.



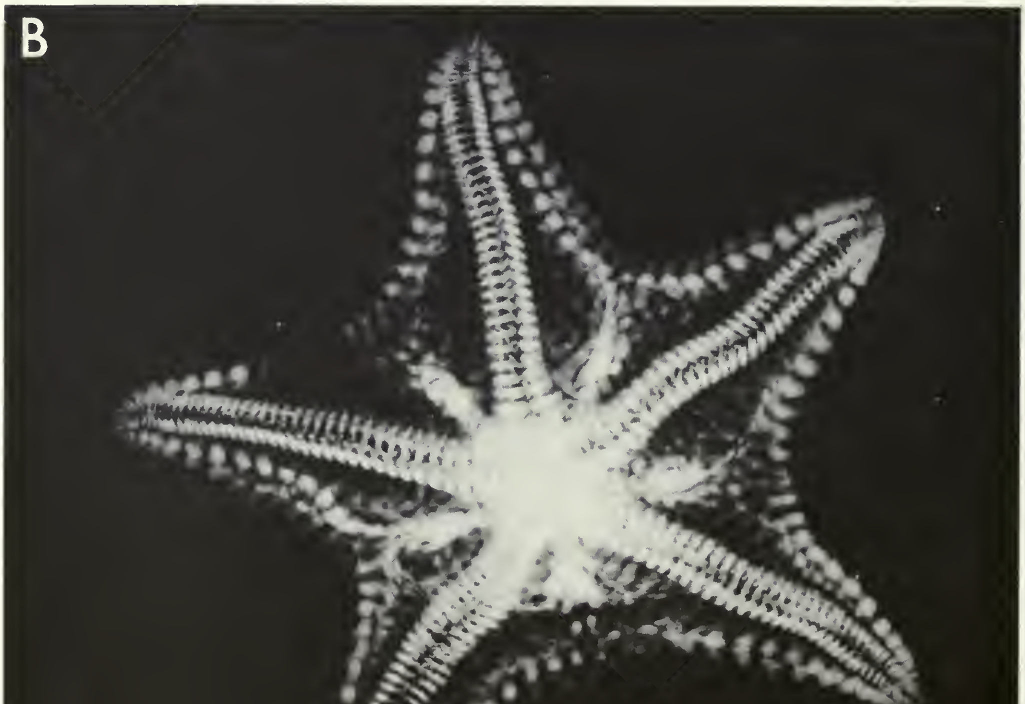


Fig. 18 X-rays of *Porania* (*Porania*) *pulvillus* (O. F. Müller): A (as in 5C); B, 1981.3.24.28, Rockall Bank, R 55 mm (the inferomarginal spines only show in one interradius though in fact present in the others; a section of one arm removed). × 1½.

5 metres (a new record from Lunna, Shetland Is where it was collected by a diver) and a maximum of *c.* 250 metres, whereas *P. stormi* is an upper bathyal species limited to more remote areas, from S of Iceland to the continental slope W of the British Isles and possibly from N Norway.

However, there is a much closer morphological resemblance between *Porania pulvillus* and the american *P. insignis* Verrill, 1895: 138–139. The former is consistently relatively thin-walled with a well-marked ventrolateral angle. Although the available material suggests that the abactinal skeleton may be more open in the american taxon, the main difference is that some adults retain a few actinal spines whereas these are almost invariably lost at an early stage in *P. pulvillus.* Madsen (pers. comm.) has independently reached the same conclusion.

To provide a summary of the main diagnostic characters used in identification of poraniids, a tabular key to the genera and subgenera now accepted is given here (Table 2).

Table 2 Tabular key to the genera of Poraniidae. Alternate columns in lower case.

	1	2	3	4	5	6	7
Poraniopsis	W	s(i)	C–O	r	SD	q+	T
Porania (*Porania*)	W(R)	n,s(i)	O	a	SC	q+/−	T
Porania (*Pseudoporania*)	R	n	O	r	L	q−	T
Tylaster	R	i	?	r	S*(D)	q+	T
Spoladaster	R	i	O(C)	r	SD	q,p(+)	T
Chondraster	R	n	O	a(r)	H	q−[+]	M
Poraniomorpha (*Culcitopsis*)	R	i	C	r	L[M]	p−	M(T)
Poraniomorpha (*Poraniomorpha*)	W	f	C(S)	r	M	s+/−	M(T)
Marginaster	[W]	[s]	[S]	[a]	[SC]	[q−]	[T]

Note: Square brackets indicate occurrence in small specimens, as throughout in *Marginaster;* round brackets show the condition in occasional specimens or a modified form. *In *Tylaster willei* the inferomarginal spines are evidently in triangular groups of three, not a horizontal line.

1. Abactinal skeleton:
    W–well developed
    R–more or less reduced by resorption, especially in large specimens, R > 50 mm
2. Superficial dorsal body wall:
    f–with very fine continuous or clustered spinules, tubercles or papillae, not necessarily articulated to the underlying plates
    i–with fine isolated spinules, not articulated to the plates
    n–naked and smooth, sometimes with surface spicules so dense as to show a pale colour when dried
    s–with spaced relatively large spines mounted on the larger plates or vestiges of plates
3. Papulae:
    C–clustered
    O–in open groups, short arcs or evenly spaced over wide areas
    S–single
4. Shape of margin:
    a–more or less distinctly angular ventrolaterally, corresponding to the horizontally projecting inferomarginals
    r–rounded, the inferomarginals hardly, if at all, projecting or else both series of plates reduced
5. Inferomarginal armament:
    H–hidden in live or well-preserved specimens, the few large spines wholly within the much thickened body wall
    L–lacking altogether
    M–of multiple spinelets clustered along the ventrolateral convexity
    S–of up to 5 large spines in a horizontal row, at least their tips projecting, forming either a continuous fringe (C) or a discontinuous grouped series (D)
6. Appearance of actinal areas (apart from the ciliated grooves between the furrows and margins):
    p–pustular
    q–quite smooth (apart from any macroscopic armament)
    s–with fine superficial spinules, usually slightly spaced
    +/− with or without enlarged spinelets or spines in series parallel to the inferomarginals
7. Adambulacral armament:
    T–arranged normally in one series transverse to the furrow, usually 2 or 3 spines
    M–with multiple furrow spines on most plates, subambulacral spines variously arranged, paired, in an oblique but nearly longitudinal series within a common sheath, or transversely

Nomenclature

The classification of the Poraniidae has been complicated not only by the thick skin obscuring the usual diagnostic characters afforded by the skeleton but also by failure to allow for ontogenetic changes and an unwise propensity of certain early workers to give new names to juvenile or small specimens. Consequently, the names of certain species-group taxa are threatened by the possibility that they will be proved to be synonymous or homonymous with prior nominal species, as follows:

Poraniomorpha (Culcitopsis) borealis (Süssbach & Breckner, 1911) is threatened by two possibilities, firstly:

Asterina borealis Verrill, 1878 (holotype extant in the Peabody Museum, Yale, R 12 mm), long synonymized with *P. hispida,* may prove to be consubspecific with *P. (Poraniomorpha) hispida rosea* Danielssen & Koren, 1881, which it antedates. In this eventuality and if the subspecies now proposed is accepted, then *borealis* Verrill would be a senior species-group homonym within the genus *Poraniomorpha.*

Secondly:

Marginaster pentagonus Perrier, 1882 (holotype extant in the Paris Museum, R only 3 mm) may prove to be a senior synonym. The name *pentagonus* has only been mentioned as a possible synonym since Perrier, 1894.

Porania pulvillus insignis Verrill, 1895 is threatened by:

Asterina pygmaea Verrill, 1878 (holotype extant in the Peabody Museum, R only 5 mm), which may prove to be a senior synonym. The name *pygmaea* has been unused since referred to *Poranisca* by Verrill, 1914.

Porania antarctica Smith, 1876 is threatened by:

Astrogonium fonki Philippi, 1858, which Madsen (1956) has little doubt was based on specimens conspecific with *P. antarctica magellanica* Studer, 1876 but which he assumed are no longer extant in any chilean collection since they were not mentioned in Meissner's note on Philippi's asteroids of 1898. The name *fonki* has been unused since 1858 but *P. antarctica* is widely utilized.

Summary of taxonomic confirmations or changes

Poraniella Verrill, 1914, referred to the family Asteropseidae from Poraniidae.

Poraniopsis Perrier, 1891, referred to the family Poraniidae from Echinasteridae.

Poranisca Verrill, 1914, with type species *P. lepidus* Verrill, 1914, synonyms of *Marginaster* Perrier, 1881 and *M. pectinatus* Perrier, 1881.

Chondraster Verrill, 1895, confirmed as of generic rank, distinct from *Porania* Gray, 1840.

Poraniomorpha rosea Danielssen & Koren, 1881, treated as a subspecies rather than a form or variety of *P. hispida* (M. Sars, 1872).

Culcitopsis Verrill, 1914, type species *Culcita borealis* Süssbach & Breckner, 1911, treated as subgenus of *Poraniomorpha* Danielssen & Koren, 1881.

Culcitopsis borealis (Süssbach & Breckner), treated as a separate species rather than a form of *Poraniomorpha hispida* (M. Sars).

Sphaeriaster Dons, 1939, type species *Sphaeraster berthae* Dons, 1938, synonyms of *Poraniomorpha (Culcitopsis)* Verrill and *P. (C.) borealis* (Süssbach & Breckner).

Tylaster meridionalis Mortensen, 1933, confirmed as a synonym of *Spoladaster brachyactis* (H. L. Clark, 1923).

Pseudoporania Dons, 1936, type species *P. stormi* Dons, 1936, a subgenus of *Porania* Gray.

Porania insignis Verrill, 1895, reduced to a subspecies of *P. pulvillus* (O. F. Müller).

Taxa the affinities of which need further investigation:

Asterina borealis Verrill, 1878 and *Porania spinulosa* Verrill, 1880, as infraspecific taxa within, rather than pure synonyms of, *Poraniomorpha hispida* (M. Sars).

Marginaster austerus Verrill, 1899, in relation to *M. pectinatus* Perrier.

Marginaster fimbriatus Sladen, 1889, in relation to *Chondraster grandis* (Verrill, 1878).

Marginaster pentagonus Perrier, 1882, in relation to *Poraniomorpha hispida borealis* (Süssbach & Breckner).

Sphaeriaster bjoerlykkei (Dons, 1938), in relation to *Poraniomorpha hispida borealis* (Süssbach & Breckner) *and P. tumida* (Stuxberg, 1878).

Tylaster Danielssen & Koren, 1881, with type species *T. willei* Danielssen & Koren, 1881, in relation to *Chondraster* Verrill, 1895 and *Porania* Gray.

Spoladaster Fisher, 1940, with type species *Cryaster brachyactis* H. L. Clark, 1923, in relation to *Poraniomorpha* Danielssen & Koren.

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The larval and post-larval development of the Thumb-nail Crab, *Thia scutellata* (Fabricius), (Decapoda: Brachyura)

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Introduction

The Thumb-nail crab, *Thia scutellata* (Fabricius) has been reported from the west coast of Sweden, off German, Belgium and Netherlands coasts, in the southern North Sea, from western sea areas of the British and Irish coasts, and southwards to the Mediterranean and west coast of Africa (see Christiansen, 1969; Ingle, 1980; Manning & Holthuis, 1981). The larval and early crab stages have been figured by Claus (1876), Cano (1892), Lebour (1928) and Williamson (1915). Except for Claus, these authors also gave very brief descriptions of stages, Williamson's being based on Claus' and Cano's figures; the accounts relate chiefly to plankton caught material and are somewhat superficial.

In 1975 Mr T. Farrall, a Deputy Head of Langdon Park School, London, obtained two ovigerous crabs of *T. scutellata* from the Channel Islands while studying the relationships of this species with the Purple Heart Urchin, *Spatangus purpureus* O. F. Muller. The live crabs were donated to the British Museum (Natural History) and the eggs of one hatched on 18th September 1975. Sufficient material was reared through to fifth crab stage to enable a complete account to be given of the larval and early post-larval development of this species in the laboratory.

Materials and methods

The female, from which the larvae and post-larvae were reared, was collected near Vermerette Rock, Herm, Channel Islands in September 1975. The larvae were reared using methods described by Rice & Ingle (1975) and Ingle & Clark (1977). All material was fixed and stored in the preservative formulated by Steedman (1976: 148) and later transferred to 70% alcohol. Drawings and measurements were made with the aid of a *camera lucida*. Measurements are as follows: T. T. = total lengths of zoeae, measured between tips of dorsal and rostral spines; C. L. = carapace lengths, measured from between eyes to posterio-lateral carapace margin for zoeae, from rostral tip (for megalopa) and from frontal margin (for crab stage), to median posterior margin of carapace.

The female and reared material are deposited in the Collections of the Zoology Department, British Museum (Natural History), registration number: 1983:312.

Descriptions

Thia scutellata (Fabricius, 1793)

Thia polita: Claus, 1876: 56, Tav. X, figs 1–7 (1st zoea); Cano, 1892: 7, Tav. II, figs 16–26 (A–E) (1st–3rd zoeae, megal. 1st crab); *Thia residuus*: Williamson, 1915: 548–50, figs 470–479 (1st and later zoeae, megal. after Claus & Cano); *Thia polita:* Lebour, 1928: 528–9 (1st-4th zoeae, megal. 1st crab described), fig. 5 (17), Pl. I, fig. 11 (2nd zoea, coloured), Pl. VIII, figs 7–8 (3rd zoeae, megal. 1st, 2nd crab); Bourdillon-Casanova, 1960: 167.

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First zoea

Dimensions: T. T. 2·70 mm, C. L. 0·70 mm.

Carapace (Fig. 1a): Dorsal spine long and straight, stout proximally and narrowing distally; rostral spine thinner than dorsal and shorter; lateral spines about $\frac{1}{3}$ carapace length; dorso-median elevation present; carapace dorsal margin slightly elevated, a pair of prominent posterio-median setules present.

Eyes: Partly fused to carapace.

Antennule (Fig. 2b): Unsegmented, with 3 terminal aesthetascs and 2 setae.

Antenna (Fig. 2f): Spinous process about $2\frac{1}{2}\times$ length of exopod, distal $\frac{1}{2}$ spinulate; exopod with 1 long and 1 short seta.

Mandible (Fig. 2i): Incisor not differentiated from molar process.

Maxillule (Fig. 2l): endopod 2-segmented, with 1,6 setae; basal endite with 5 and coxal with 7 setae/spines.

Maxilla (Fig. 3c): endopod with broad outer and narrower inner lobe with 5+3 setae; basal endite with outer lobe slightly broader than inner, with 4+5 setae; coxal endite with outer lobe slightly broader than inner, with 4+3 setae; scaphognathite with 4 plumose setae and a very stout posterior plumose projection.

First maxilliped (Fig. 4a): Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 2,2,1,2,4+1 setae; exopod incipiently segmented with 4 terminal plumose setae.

Second maxilliped (Fig. 4c): Basis with 4 setae; endopod 3-segmented with 1,1, 3+1 setae; exopod with 4 terminal plumose setae.

Third maxilliped: Not developed.

Pereiopods: Not developed.

Abdomen (Figs 1e, 2a): 5 segmented+telson; 2nd segment with a pair of dorso-lateral processes; posterio-lateral margin of 1st truncate, of 2nd–5th rounded to sub-acute and minutely spinulate. A pair of small setae near posterio-dorsal margin of segments 2–5. Telson forks long and thin, each with thin long lateral and dorsal spine; inner medio-lateral margin of telson with 6 setae all similarly plumed; median margin of telson strongly concave.

Second zoea

Dimensions: T. T. 3·1 mm, C. L. 0·75 mm.

Carapace (Fig. 1b): Posterior margin with 3–4 long setules; two pairs of dorso-median setae now present.

Eyes: Now stalked.

Antennule (Fig. 2c): Now with 6 acesthetascs and 1 seta.

Antenna: Unchanged.

Mandible: Unchanged.

Maxillule (Fig. 2m): Endopod setation unchanged; outer margin of basal endite with a prominent plumose seta, dorso-inner margin with 9 setae/spines; coxal setation unchanged.

Maxilla (Fig. 3d): endopod setation unchanged; basal endite with 5+5 setae and additional seta in some specimens (some distance from margin); coxal setation unchanged; scaphognathite with 11 plumose marginal setae.

First maxilliped: Basal and endopod setation unchanged; exopod with 6 terminal plumose setae.

Second maxilliped (Fig. 4d): Basal setation unchanged; endopod with 1,1, 4+1 setae; exopod with 6 terminal plumose setae.

Third maxilliped: Not developed.

Pereiopods: Not developed.

Abdomen (Fig. 1f): Sixth segment incipient; 1st segment with dorso-median setule; dorsal-lateral processes on 2nd segment less acute and not curved. Inner medio-lateral margin of telson with additional pair of small setules; lateral spine on telson reduced to a very minute setule.

THIRD ZOEA

Dimensions: T. T. 3·8 mm, C.L. 1, 30 mm.
Carapace (Fig. 1c): Posterior margin with 5 long setules; three pairs of dorso-median setae now present.
Eyes: Unchanged.
Antennule. (Fig. 2d): two or 3 of the 6 aesthetascs now sub-distal.
Antenna (Fig. 2g): Spinous process slightly less than 3× length of exopod; endopod now developed as a conspicuous bud.
Mandible (Fig. 2j): Incisor and molar processes now differentiated.
Maxillule (Fig. 3a): Endopod setation unchanged; basal endite with 11 and coxal with 10 setae/spines.
Maxilla (Fig. 3e): Endopod, basal and coxal endite setation unchanged; scaphognathite with 18 setae.
First maxilliped (Fig. 4b): Basal setation unchanged; endopod terminal segment now with 5+1 setae; exopod with 8 terminal plumose setae.
Second maxilliped: Basal and endopod setation unchanged; exopod with 8 terminal plumose setae.
Third maxilliped: Represented as a small bud.
Pereiopods: now represented as small buds.
Abdomen (Fig. 1g): Sixth segment now fully differentiated; first segment with 3 conspicuous dorso-median setules; innermost pair of medio-lateral setules on telson much longer than in previous stage; pleopods represented as conspicuous buds on segments 2–5.

FOURTH ZOEA

Dimensions: T.T. 4·6 mm, C.L. 1·60 mm.
Carapace (Fig. 1d): Dorsal and rostral spines stouter than in previous stage and lateral spines smaller; posterior margin of carapace with 11–12 setules.
Eyes: Unchanged.
Antennule (Fig. 2e): Incipiently 2–3 segmented, ultimate segment with 2 aesthetascs and 1 seta, penultimate with 7 distal and 2 sub-distal aesthetascs; endopod bud developed.
Antenna (Fig. 2h): Spinous process about 2½× length of exopod; innermost terminal seta of exopod very long; endopod bud very long.
Mandible (Fig. 2k): Now with incipient palp.
Maxillule (Fig. 3b): Endopod setation unchanged; basal endite now with 16 setae/spines; coxal setation unchanged.
Maxilla (Fig. 3f): Endopod setation unchanged; basal endite with 6+6–7 setae; coxal setation unchanged.
First maxilliped: Basal and endopod setation unchanged; exopod with 10 distal plumose setae.
Second maxilliped: Basal and endopod setation unchanged; exopod with 10 distal plumose setae.
Third maxilliped: now bilobed.
Pereiopods: longer than previous stage and cheliped dactylus differentiated.
Abdomen (Fig. 1h): Dorsal surface of telson with a pair of small setules; pleopod buds well developed, longer than in previous stage.

MEGALOPA

Dimensions: C.L. 2·2 mm.
Carapace (Fig. 4e,f): Longer than broad; frontal region broad, margins almost parallel; a small median furrow near rostral base; rostrum slightly deflected ventrally; cardiac region with suggestion of a broad tubercle; posterior margin with numerous setae.
Eyes: Large.
Antennule (Fig. 5a): Peduncle 3-segmented, setose as shown exopod incipiently 3-segmented, with 4,4,4,–5 aesthetascs and 0,1,2 setae respectively; endopod incipiently 2-segmented with 5 terminal setae.

Antenna Fig. 5b): Peduncle 3-segmented, with 0,2,1 setae respectively; flagellum 8-segmented with 4,0,2,0,4,0,3,4 setae respectively.
Mandible (Fig. 5c,d): Molar and incisor processes not differentiated; mandibular palp (d) 3-segmented, terminal segment long and slightly curved, with 8 setules.
Maxillule (Fig. 5e): Endopod long and unsegmented, with 2 sub-terminal and 2 terminal setae all reduced; basal endite with 23–24 setae/spines; coxal endite still with 10 setae/spines.
Maxilla (Fig. 5f): Endopod now reduced to a sub-acute lobe with 1–2 setae; basal endite with 7+7 setae, coxal still with 4+3 setae; scaphognathite with 41–42 plumose setae, shorter than in last zoeal stage.
First maxilliped (Fig. 5g): Coxal and basal segments slightly differentiated coxal with 11–12 setae on or near inner margin; basis with 28–29 setae; endopod unsegmented and with 3 distal setae; exopod 2-segmented, distal segment with 3 terminal setae; epipod (not shown) with 3–4 setae.
Second maxilliped (Fig. 5h): Coxal and basal segments undifferentiated; endopod with only propodus and dactylus demarcated, propodus with 6 setae, dactylus with 5 spines+1 seta; exopod 2-segmented, distal segment with 3 setae; epipod (not shown) short, with 2–3 setae.
Third maxilliped (Fig. 5i): Inner margin of coxa with 1 and basis with 4 setae; inner margin of ischium with 3–4 small denticles and with 10–11 setae, carpus-dactylus with 7,5,6,4–5 setae respectively; epipod (not shown) long and with 10–11 setae.
Pereiopods (Fig. 6a–f): Cheliped stout, setose as shown, propodal palm inflated, inner propodal and dactylar margins cut into irregular teeth (b); cheliped without coxal or ischial spines. Pereiopods 2–5 (c–f) short and stout, setose as shown, dactyls terminally very acute and those of 5th with 2 long terminal simple setae in addition to 3 prominent, slightly shorter ones on lower margin.
Abdomen (Fig. 4g,h, 6g): With 6 segments+telson and setose as shown, posterio-lateral margins broadly truncate. Telson (Fig. 6g) truncate, about as broad as long, dorsal surface with 2 pairs of median setules. Five pairs of pleopods, exopods with long plumose marginal setae, 1st (Fig. 6h) with 13, 2nd 15, 3rd 14, 4th (Fig. 6i) 11, 5th (uropod, Fig. 6g) with 8 setae respectively; endopods of pleopods 1–4 each with 3 distally placed coupling hooks on internal margins.

FIRST CRAB
Dimensions: C.L. 2·54 mm.
Carapace (Fig. 6j): Longer than broad, frontal region projecting; four pairs of anterio-lateral teeth, 1st-3rd acute, 4th small and obtuse. Dorsal surface of carapace smooth and anteriorly with minute setules; margins with well developed plumose setae.

Remarks

The present laboratory reared material of *Thia scutellata* agrees in most aspects with previous accounts of the larval and post-larval descriptions of this species (see p. 53), except in the following features. (1) The maxillule of the 1st zoea figured by Claus (1876) shows 1+5 setae on the endopod and 4 on the coxa and the setal formula for the maxilla is given as 5+2, 3+4, 2+3 for endopod, basis and coxa respectively; Claus also figured an incipient 3rd maxilliped in this 1st stage zoea. (2) Lebour (1928) depicts 2 dorsal setules on the 1st abdominal segment of the 3rd zoea whereas all the present specimens have 3 setules. (3) Lebour did not examine 1st stage zoeae and assumed that only one spine was present on each telson fork in this stage although Claus clearly shows two spines in his figure of the 1st zoea. In the present material the lateral spine is minute from the 2nd zoeal stage onward. However, Cano (1892) depicted two prominent spines on the telson forks of the zoea that he attributed to the 3rd stage of *T. scutellata.* (4) In all previously published figures of the 1st crab stage the carapace anterio-lateral margins are shown as more prominent than observed in the present material and Lebour figured these margins as somewhat irregular in outline.

The zoea of *Thia scutellata* can be distinguished from those of other brachyrhynchs (except perhaps *Atelecyclus,* see below) described from NE. Atlantic waters on the following combined features. (1) Lateral spines on carapace. (2) Dorso-lateral processes confined to 2nd abdominal segment. (3) Two setae on basal segment of 1st maxilliped endopod. (4) Lateral spine on telson forks reduced to a very minute setule in 2nd-4th stages. The megalopa of *T. scutellata* is less easy to recognize because this stage is inadequately described for many species of NE. Atlantic brachyrhynchs. *T. scutellata* megalopa has the following combined features. (1) Absence of coxal or ischial spines on the pereiopods. (2) Sternites without spines. (3) Absence of tubercles or spines on carapace. (4) Uropod with 8 setae. (5) The two long terminal setae on the dactylus of the fifth pereiopod have simple apices.

Lebour (1928: 528) proposed the family name Thiidae for *Thia polita,* stating that this species is 'different in many ways, and its larval stages does not fit into any family, although apparently near the Cancridae and the Corystidae'. The family name is now accredited to Dana 1852. Rice (1980: 333), basing his remarks on Lebour's account, suggested that *Thia* is possibly more closely allied to *Corystes* than to cancrids or portunids but was unable to comment further because of the absence of adequately described material. The zoeae of *T. scutellata* have two setae on the basal segment of the first maxilliped endopod, six setae on the distal segment of the maxillule, ten setae on the basis of the first maxilliped, lateral spines on the carapace, 5+3 setae on maxilla endopod and the dorso-lateral processes confined to the second segment of the abdomen. These features place them near to the Portunidae and in this respect they key satisfactorily to that part of the key to the brachyuran families as constructed by Rice (1980: 360). Differences separating zoeae of *Thia* from *Atelecyclus* must await a critical re-examination of zoeae of *A. rotundatus* since the character listed by Lebour (1928: 487) for separating zoeae of these two genera, i.e. the presence of only one spine on the telson forks in *Thia*, is no longer valid.

Addendum

Mr José Paula, Faculdade de Ciências, Lisbon, has recently informed me that a minute third spine is present on the outer telson fork of *T. scutellata* zoeae collected in Portuguese waters. A re-examination of the present reared material has revealed that this third lateral spinule is just discernible in some specimens.

Acknowledgements

I wish to express my sincere thanks to Mr T. Farrall for kindly providing the ovigerous specimens of *T. scutellata* and to Dr A. L. Rice for reading the manuscript.

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Fig. 1 (p. 59) *Thia scutellata* (Fabricius): a–d, right lateral aspecies of 1st–4th zoeae; e–h, abdomens from dorsal aspects of 1st–4th zoeae. Scale (e–h) = 0·1 mm.

Fig. 2 (p. 60) *Thia scutellata* (Fabricius): a, lateral margins of abdominal segments 1–5 of 1st zoea; b–e, antennules of 1st–4th zoeae; f–h, antennae of 1st, 3rd & 4th zoeae; i–k, mandibles from dorsal aspects of 1st, 3rd and 4th zoeae; l, m, maxillules of 1st & 2nd zoeae. Scales = 0·1 mm, a, l, m to lower; i–k to middle; b–h to upper scale.

Fig. 3 (p. 61) *Thia scutellata* (Fabricius): a, b, maxillules of 3rd & 4th zoeae; c–f, maxillae of 1st–4th zoeae. Scale = 0·1 mm.

Fig. 4 (p. 62) *Thia scutellata* (Fabricius): a, 1st maxilliped of 1st zoeae; b, 1st maxilliped, terminal segments of 3rd zoeae; c, d, 2nd maxillipeds of 1st & 2nd zoea; e, dorsal aspect of megalopa; f, carapace of megalopa from right lateral aspect; g,h, abdomen from dorsal and right lateral aspects. Scales = 0·1 mm, g,h to upper; a, c, d, to middle; b to lower.

Fig. 5 (p. 63) *Thia scutellata* (Fabricius): megalopa: a, antennule; b, antenna c, ventral aspect of mandible; d, dorsal aspect of mandibular palp; e, maxillule; f, maxilla; g–i, 1st–3rd maxillipeds. Scales = 0·1 mm, g–i to uppermost; b to second; a to third; c, e, f to fourth; d to lowermost scale.

Fig. 6 (p. 64) *Thia scutellata* (Fabricius): a–i, megalopa; a–f, 1st–5th pereiopods; g, telson and uropods from dorsal aspects; h, i, 1st, 4th pleopods; j, carapace of 1st crab. Scales = 0·1 mm, a, c–f to upper; b, to middle; h, i to lower scale.

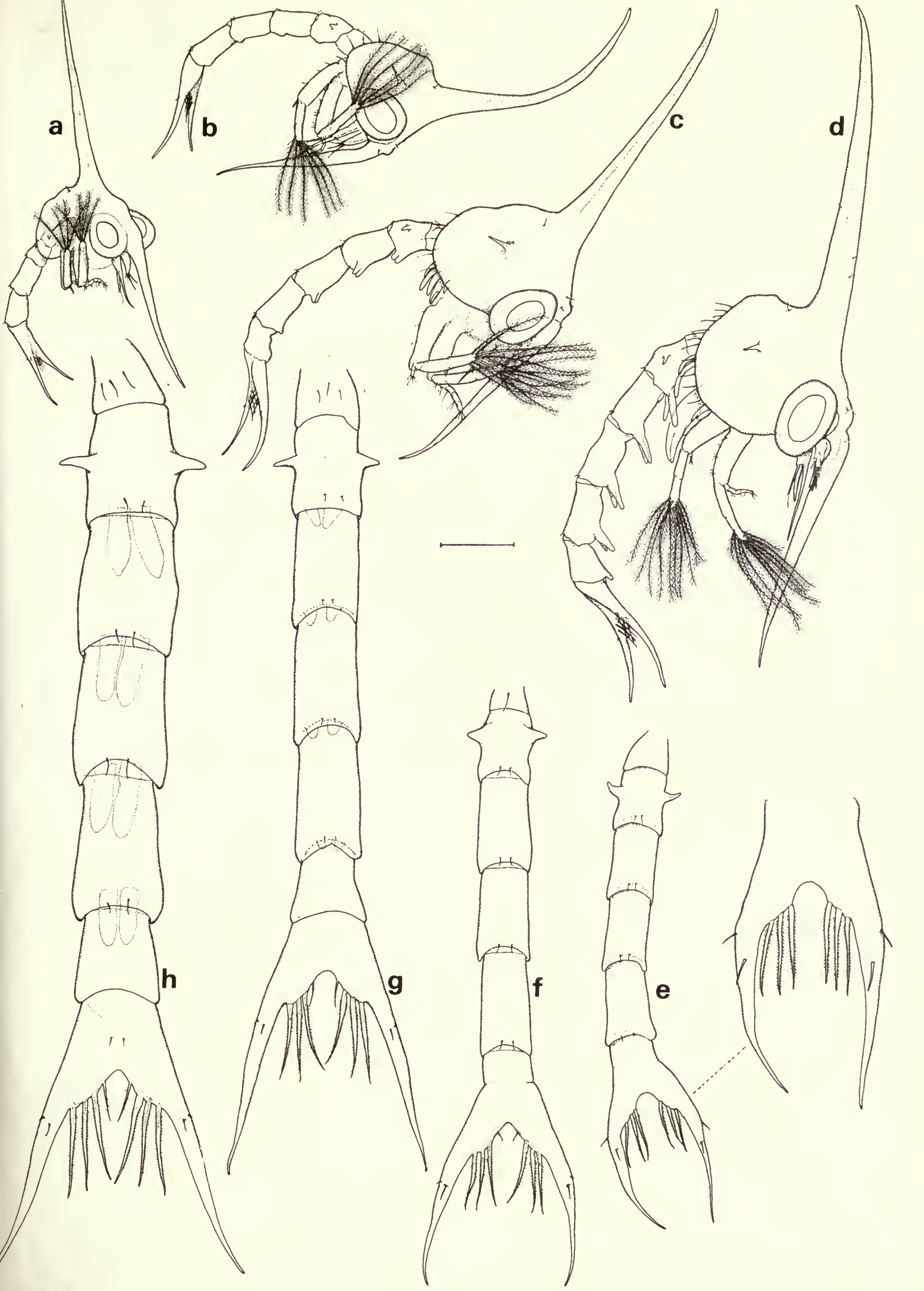

Fig. 1

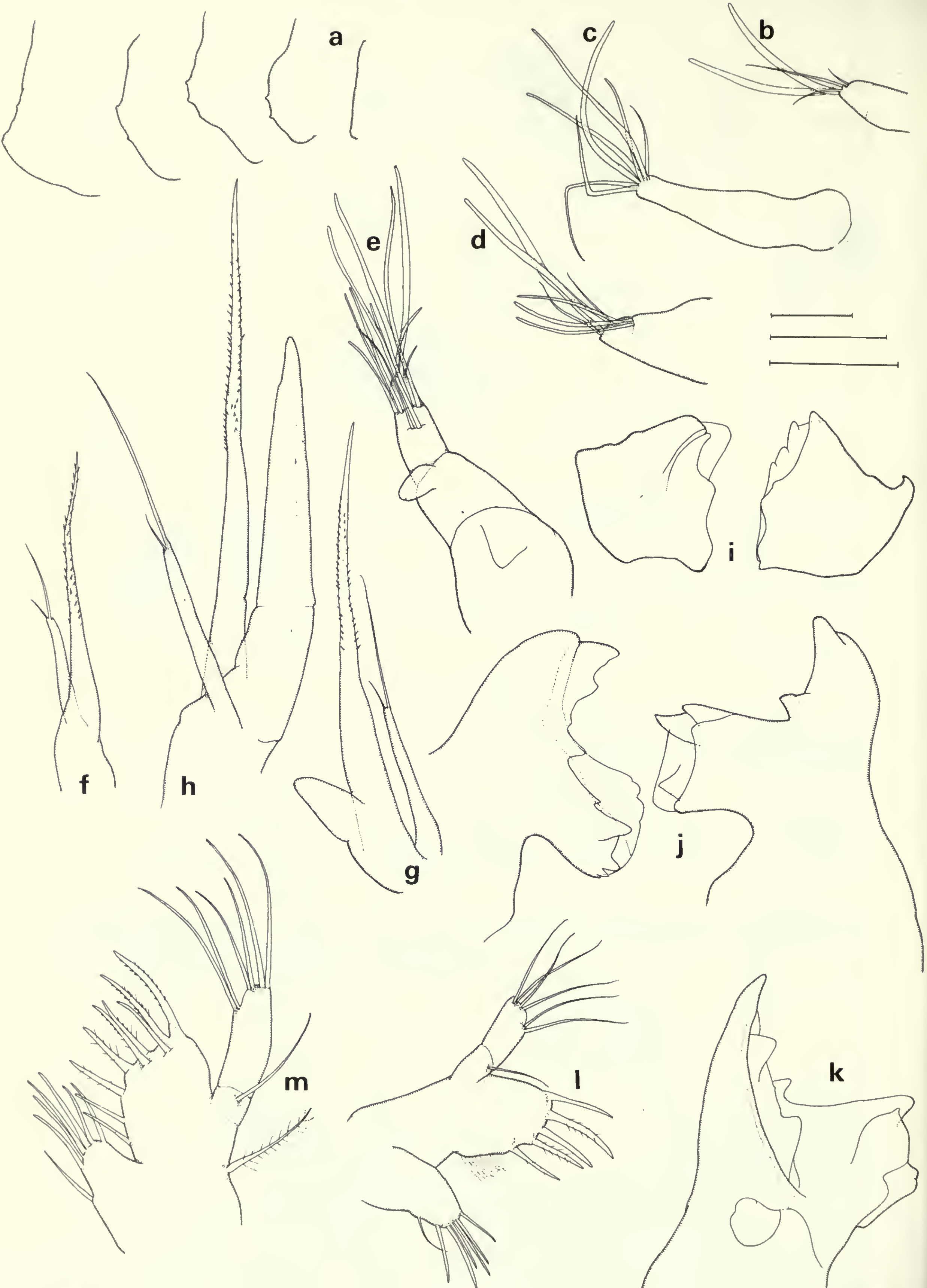

Fig. 2

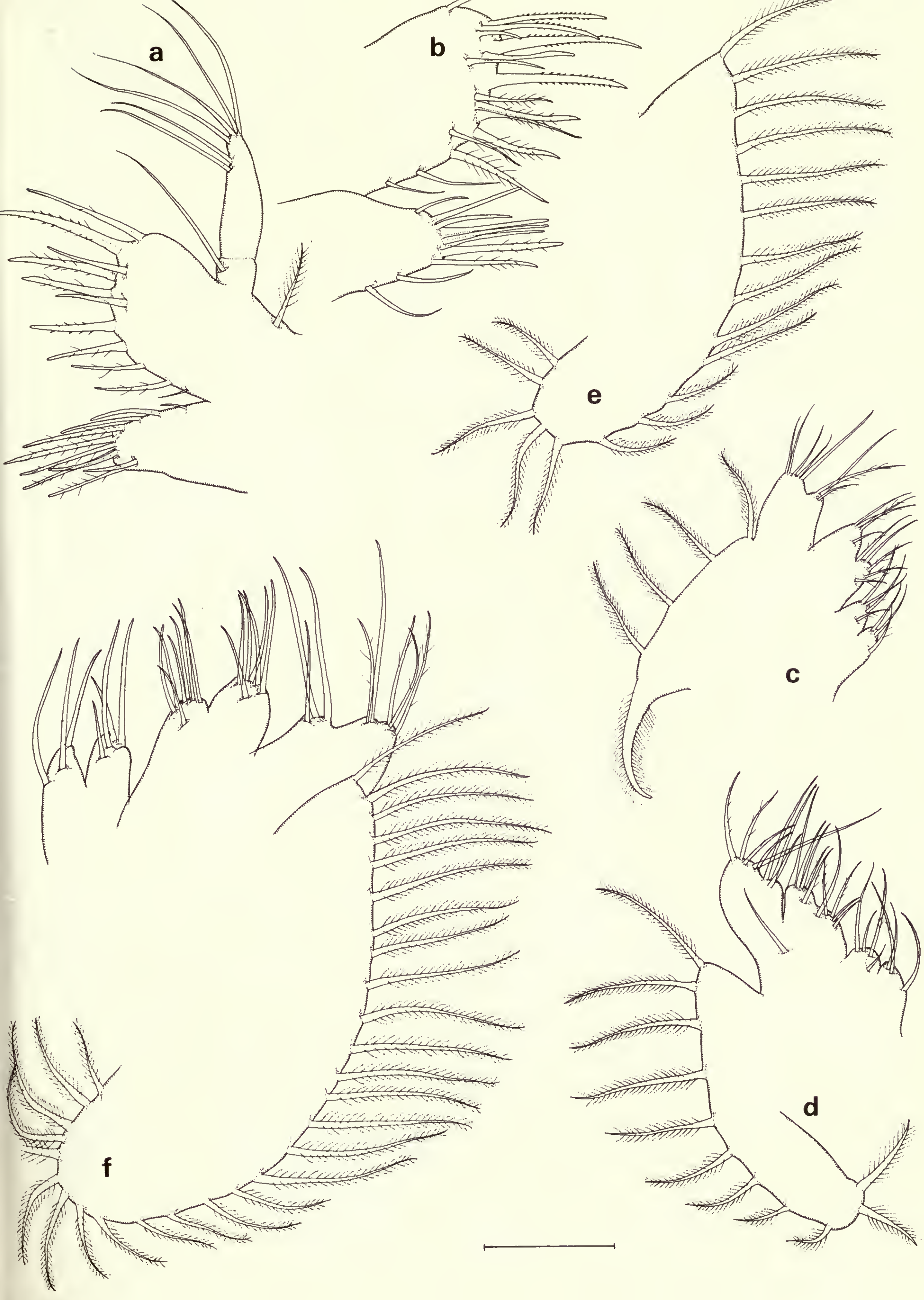

Fig. 3

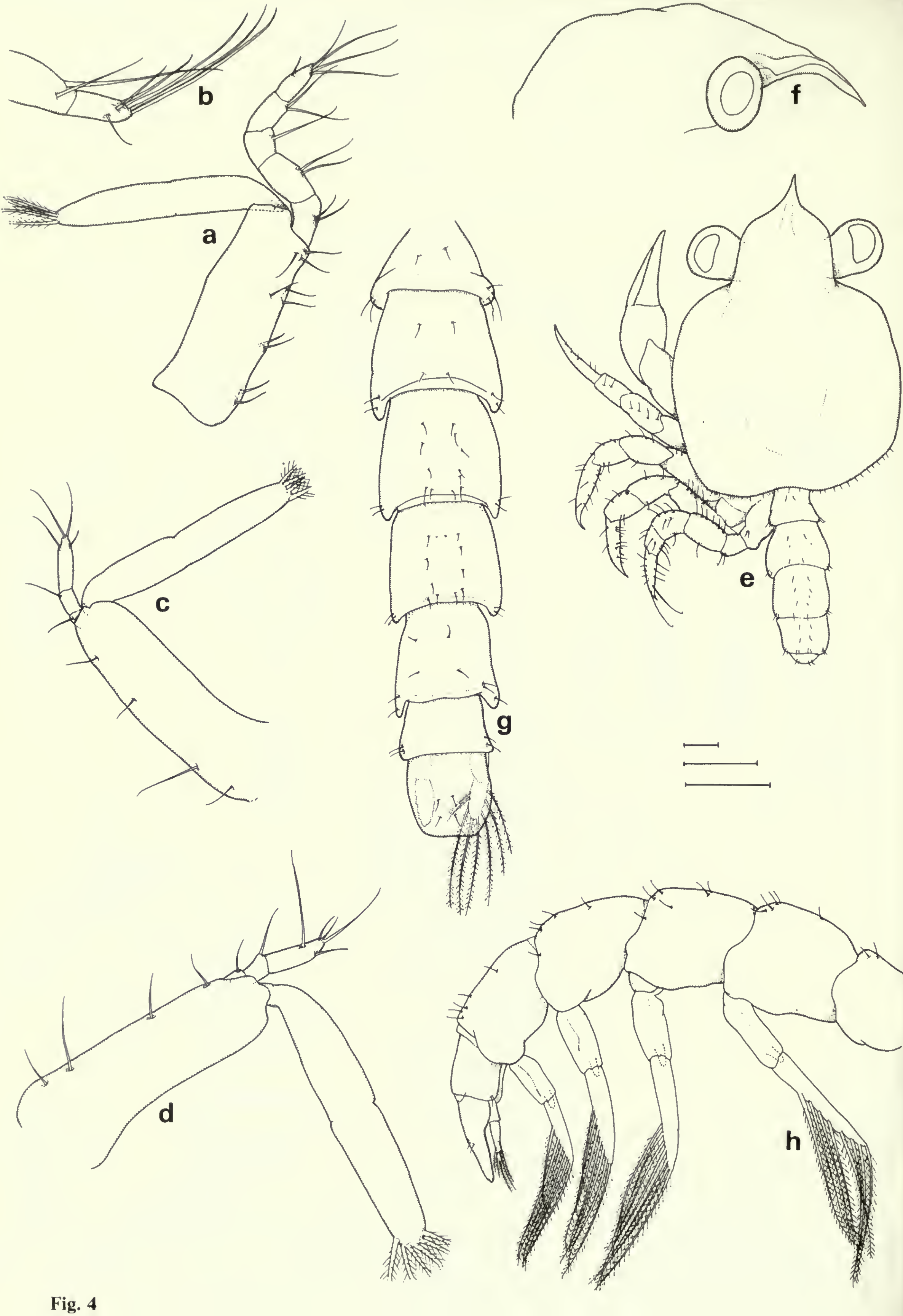

Fig. 4

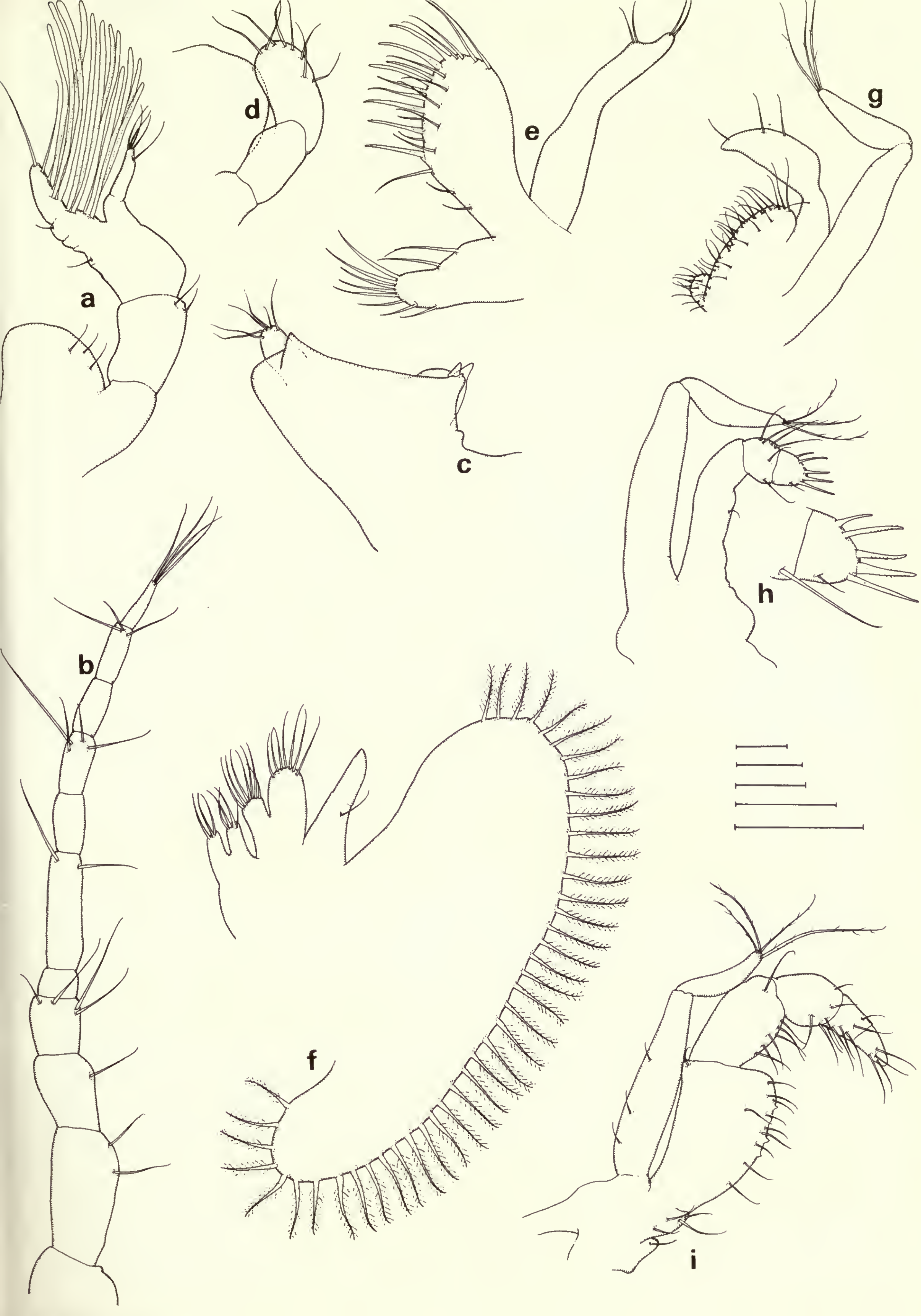

Fig. 5

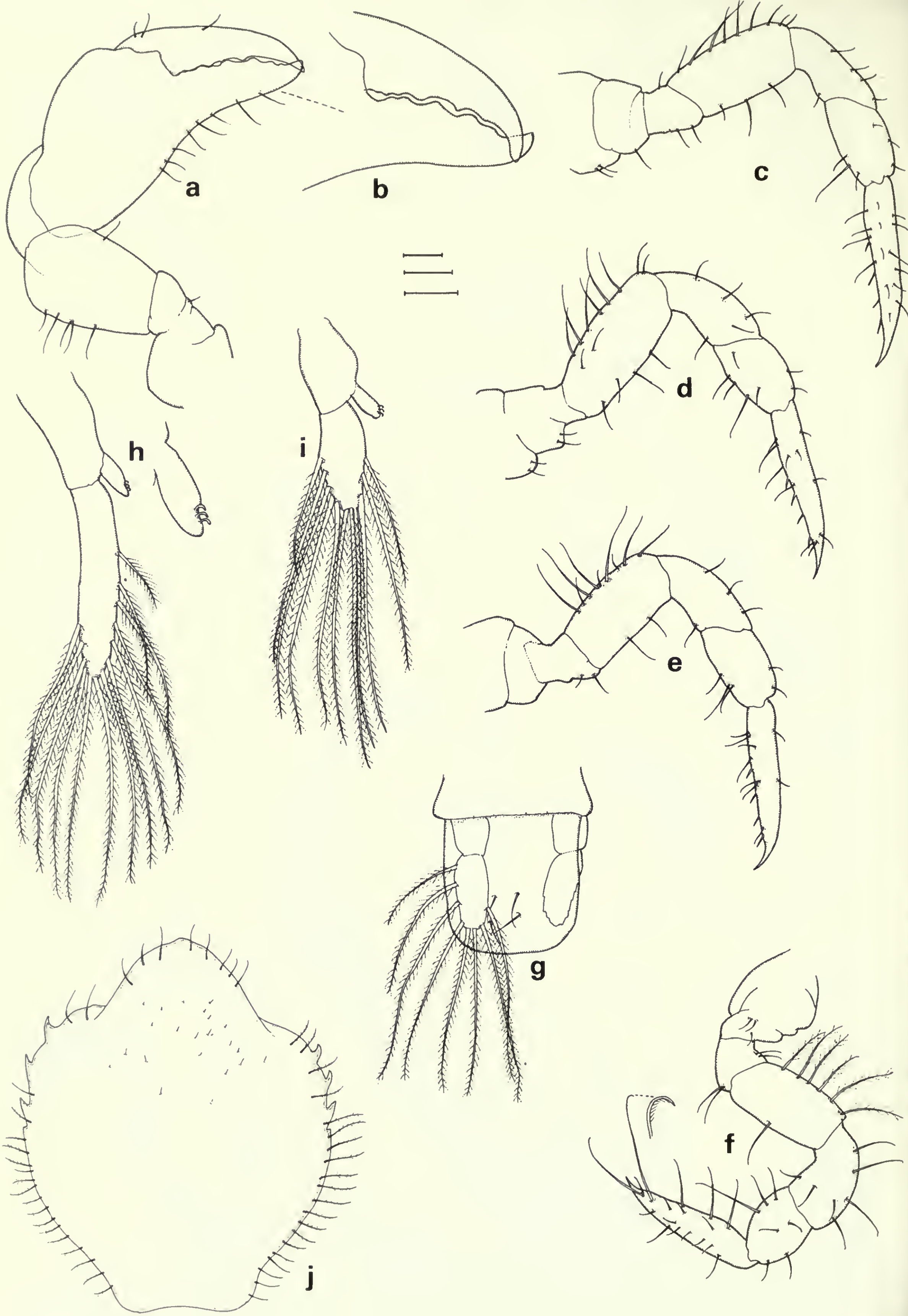

Fig. 6

Description of a new species of *Sylvisorex* (Insectivora: Soricidae) from Tanzania

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Introduction

Two species of *Sylvisorex* are known from Tanzania, *S. granti* Thomas, 1907 which has been reported from Mount Kilimanjaro and *S. megalura* (Jentink, 1888) of which specimens from three separate localities have been recorded recently by Howell & Jenkins (in press). In the course of organised collecting in Tanzania, Dr K. M. Howell of the University of Dar-es-Salaam obtained a number of shrews which were submitted to the British Museum (Natural History) for identification. These include a single example of *Sylvisorex* which on examination proves to differ substantially from all the known species of the genus in size and dental morphology, which is described here as new. The specimen differs externally from other members of the genus in the presence of bristle-hairs on the tail. The absence of such bristle-hairs has been used to distinguish *Sylvisorex* from *Suncus* but this distinction must now depend on the cranial differences elaborated by Heim de Balsac & Lamotte (1957) plus the dental characters used by Repenning (1967) and Butler & Greenwood (1979). The most readily applied of these latter characters is the presence of denticulations on the cutting surface of the first lower incisor in *Sylvisorex,* which are lacking in *Suncus*; also in *Sylvisorex* the talon of the upper premolar is more highly developed, the interorbital region broader and the braincase broader and higher relative to skull size. Additionally the hindfeet in *Sylvisorex* are larger relative to body size with slightly elongated, staggered, separated, metatarsal pads, while *Suncus* has smaller hindfeet with more oval, more or less adpressed pads.

All measurements are in millimetres: the dental nomenclature follows that of Swindler (1976), Butler & Greenwood (1979) and is illustrated in Figure 1.

Systematic Section

Sylvisorex howelli sp. nov.

Holotype. BM(NH) 82.874 adult of undetermined sex (viscera and external genitalia removed) in alcohol, skull removed; collected 27 April 1982 on Bondwa Peak, Uluguru North Forest Reserve, Uluguru Mountains, Morogoro District, Tanzania, *c.* 06°54′S 37°40′E, *c.* 1050 m on road through forest by M. K. S. Maige and donated by Dr K. M. Howell.

Diagnosis. Small, size intermediate between *S. johnstoni* (Dobson, 1888) and *S. granti;* tail with bristle-hairs; braincase shallow and long, relative to skull length; lingual edge of second upper unicuspid projecting beyond that of first, level with lingual edge of third unicuspid; crown area of fourth upper unicuspid smaller than crown area of second upper unicuspid; parastyle of upper premolar low and slender; posterolingual ridge on first lower incisor very prominent, forming a small cusp; talonid of third lower molar reduced. (See Figs 2–8).

Bull. Br. Mus. nat. Hist. (Zool.) **47**(1): 65–76

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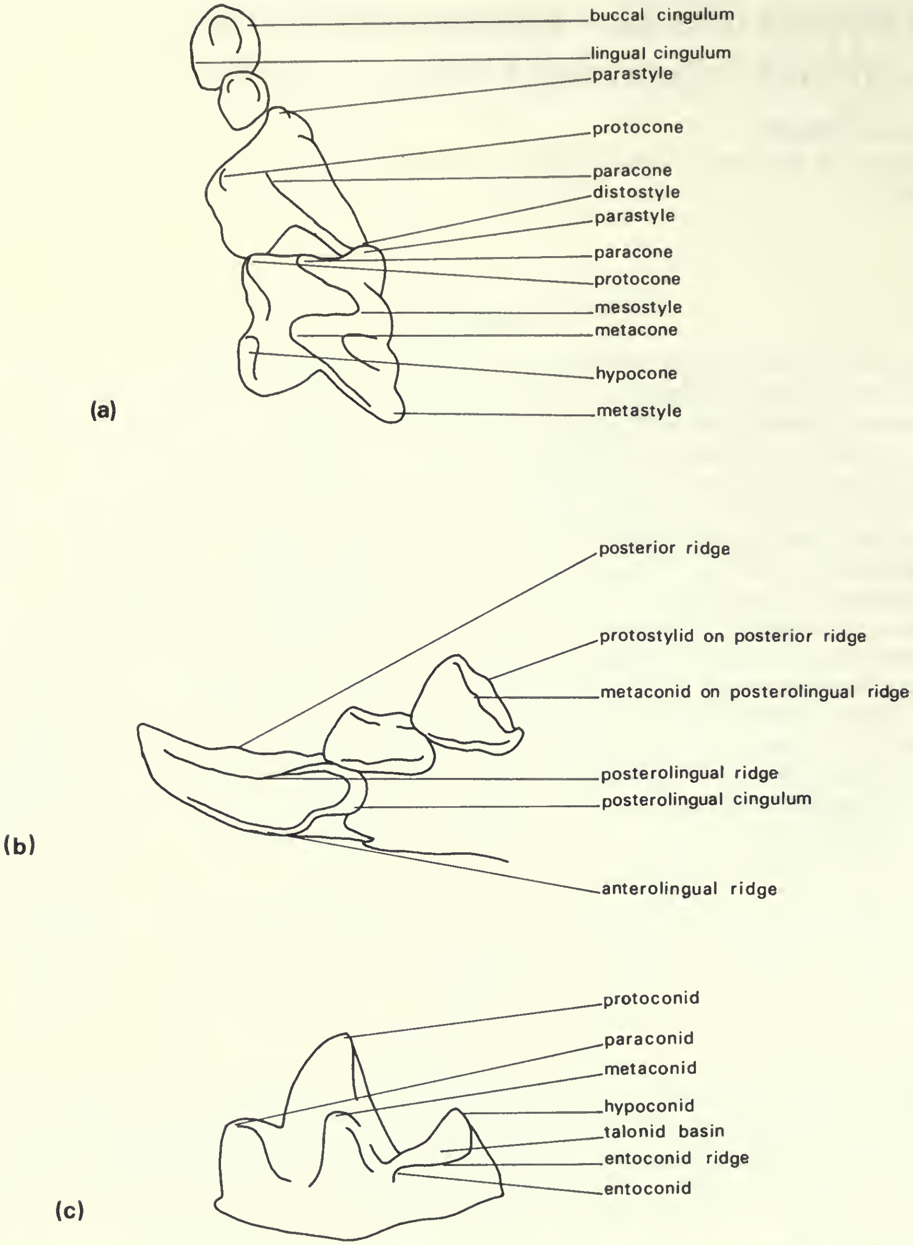

Fig. 1 Diagrams to show cusp nomenclature: (a) crown view of left upper third and fourth unicuspids, premolar and first molar; (b) lingual view of right lower first and second incisors and premolar; (c) lingual view of right lower third molar.

DESCRIPTION. Size small (head and body length 48, tail length 44·5, hindfoot length without claws 11·5, ear length 6·8); dorsally dark brown, the hairs basally grey but brown medially and terminally; ventral pelage paler brown, the hairs with light grey bases and light brown tips; a gradual transition along flanks between colour of dorsum and venter; ears, limbs and dorsal surface of tail dark brown, their ventral surfaces paler, lacking any sharp lateral demarcation; the tail with a cover of short hairs along its entire length, interspersed with longer bristle hairs on the basal two-thirds.

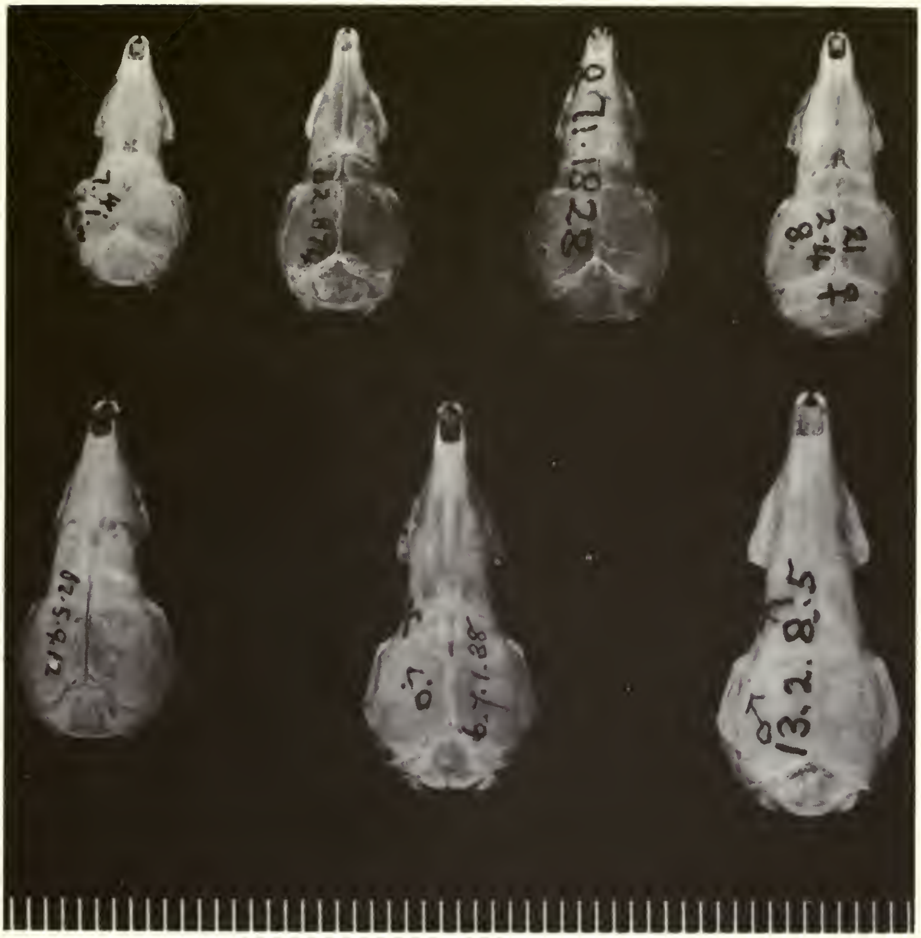

Fig. 2 Dorsal view of skulls of *Sylvisorex.* Top row from left to right: *S. johnstoni*, *S. howelli*, *S. granti* and *S. megalura*; lower row from left to right: *S. morio*, *S. lunaris* and *S. ollula.* Scale in mms.

Skull small (see Table 1), mostly lacking any exceptional features, but cranial profile sloping gradually upwards from tip of rostrum to posterior part of inter-orbital region then sloping more steeply to a rounded braincase which is long, not especially broadened and shallower relative to skull length than in other members of the genus (Figs 2–4); mandible with short, broad ascending ramus (Fig. 5).

Posterior portion of upper incisor (I^1) only slightly wider than remainder of tooth, the distance between posterior part of incisors just greater than the width of one incisor. First upper unicuspid (Un^1) sub-oval, with straight-edged lingual cingulum, tapering anteriorly and lacking any posterior cingular ridge; second upper unicuspid (Un^2) with broad lingual cingulum, approximately twice as broad as buccal cingulum, its lingual edge projecting beyond that of Un^1 and level with that of third upper unicuspid (Un^3); Un^3 with broad lingual cingulum, the tooth tapering anteriorly and rounded in crown view; fourth upper unicuspid (Un^4) with broad lingual cingulum, the tooth almost round in crown aspect and smaller than Un^2. Parastyle of upper premolar (P^4) low and slender; talon posteriorly and lingually expanded, its posterior edge level with distostyle; least internal distance between premolars (P^4–P^4) approximately three-quarters of the width of one premolar. Talon of first and second

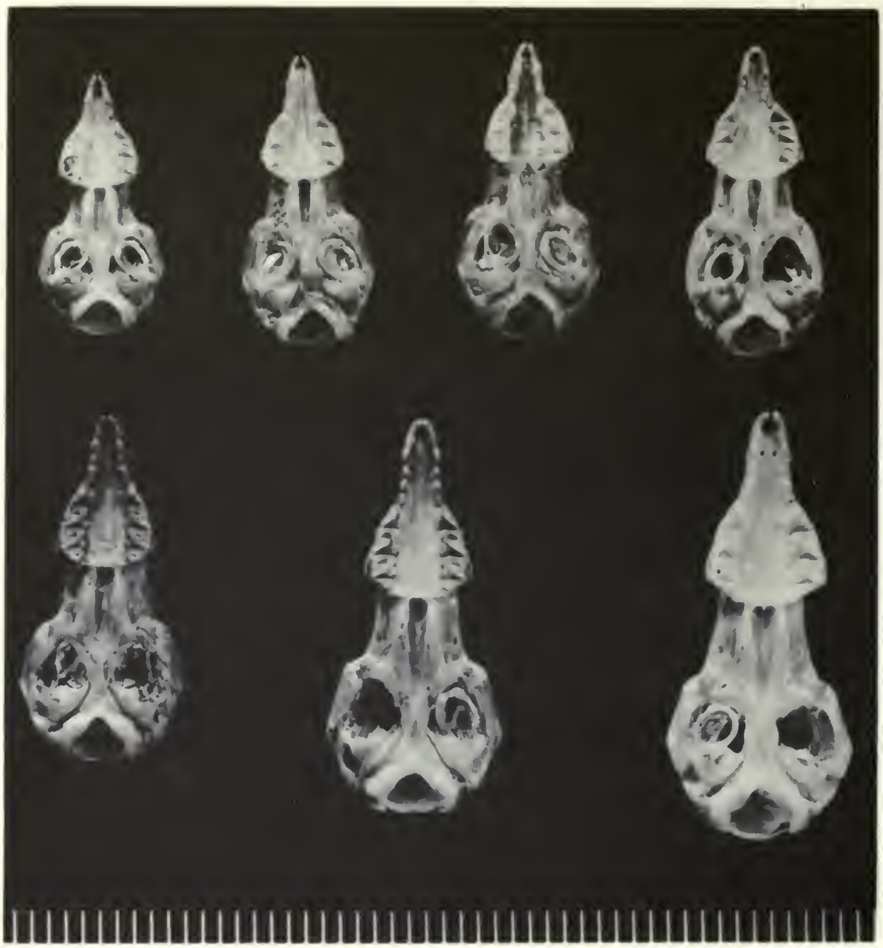

Fig. 3 Ventral view of skulls of *Sylvisorex*. Top row from left to right: *S. johnstoni, S. howelli, S. granti* and *S. megalura*; lower row from left to right: *S. morio*, *S. lunaris* and *S. ollula*. Scale in mms.

upper molars (M^1 and M^2) only slightly expanded lingually, its lingual edge straight but expanded posteriorly, so that its posterior edge is level with metastyle. Third upper molar (M^3) with a long ridge between parastyle and paracone, the ridge between paracone and protocone and that between metacone and mesostyle short, angle between protocone, metacone and midline of palate shallow; talon well-developed. Lower incisor (I_1) long, slightly curved and approximately the same vertical diameter (in lateral aspect) for most of its length, tapering gradually to its tip; two rounded elevations on posterior ridge, anterior elevation long and low; posterolingual ridge prominent, forming a small cusp, higher than posterior ridge; lingual enamel extension reaching level of protoconid of second lower incisor (I_2); lingual groove extending along length of tooth and terminating just anteriorly to notch at base of lateral enamel extension; anterolingual ridge present but poorly developed, not extending onto lateral enamel extension; no posterolingual cingulum. I_2 anteroposteriorly slightly lengthened; posterolingual ridge well-developed; no protostylid. Posterior ridge of fourth lower premolar (P_4) lacking protostylid; metaconid on posterolingual ridge barely marked. Anterior ridge of entoconid of first and second molars (M_1 and M_2) poorly developed, not divergent from lingual side of tooth, the entoconid conical; postentoconid

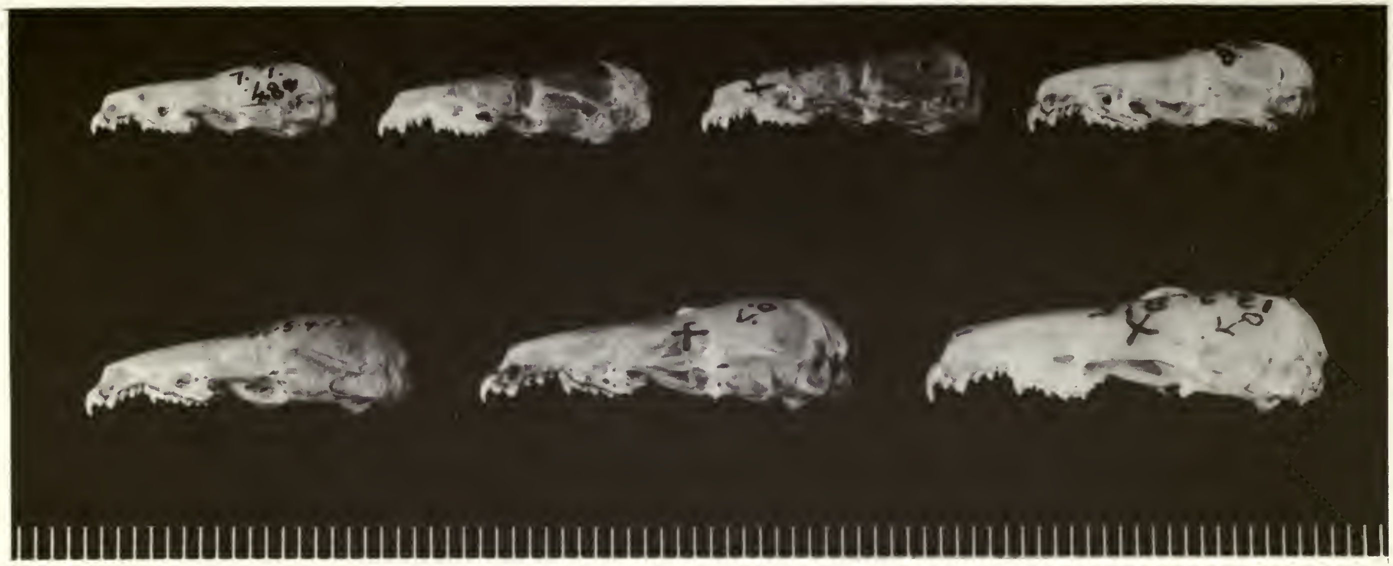

Fig. 4 Left lateral view of skulls of *Sylvisorex.* Top row from left to right: *S. johnstoni, S. howelli, S. granti* and *S. megalura;* lower row from left to right: *S. morio, S. lunaris* and *S. ollula.* Scale in mms.

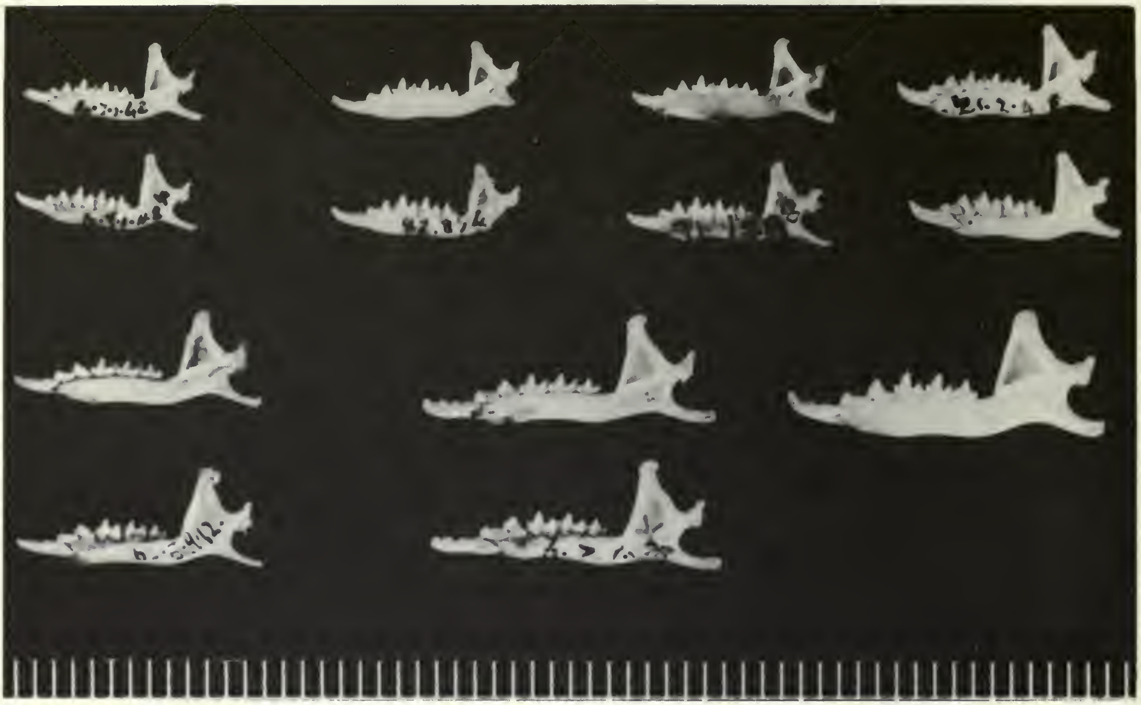

Fig. 5 Lateral view of mandibles of *Sylvisorex.* Top two rows, above—lingual view of right mandibular ramus, below—labial view of left mandibular ramus, from left to right: *S. johnstoni, S. howelli, S. granti* and *S. megalura*; lower two rows, above—lingual view of right mandibular ramus, below—labial view of left mandibular ramus, from left to right: *S. morio, S. lunaris* and *S. ollula* (left mandibular ramus absent). Scale in mms.

ledge present, adjacent to base of entoconid; lingual cingulum of M_1 weakly developed anteriorly, absent from M_2; the buccal cingulum continuing round hypoconid and merging with posterolingual rib on M_1 but on M_2 narrow and merging with posterior part of hypoconid. Talonid of third lower molar (M_3) reduced, the talonid basin reduced, the entoconid and the posterolingual rib absent but an entoconid ridge present.

ETYMOLOGY. The name of the new species is derived from that of Dr K. M. Howell of the University of Dar-es-Salaam, who kindly donated this specimen.

Comparison with other species

Key to the species of *Sylvisorex*

1. Large, condylobasal length (CBL)>23, upper toothrow length (UTL)>10 · · **S. ollula**
   Smaller, CBL <23, UTL<10 · 2
2. Larger, CBL>18, UTL>8 · 3
   Smaller, CBL<18, UTL<8 · 4
3. Larger, CBL>20, UTL>9, talonid of third lower molar (M_3) more reduced than that of second lower molar (M_2), third upper molar (M^3) anteroposteriorly compressed, $<7{\cdot}5\%$ of UTL · **S. lunaris**
   Smaller, CBL<20, UTL<9, talonid of M_3 similar to that of M_2, M^3 not anteroposteriorly compressed, $>9\%$ of UTL · · · · · · · · · · · · · · · · · **S. morio**
4. Tail longer than head and body, braincase narrow, braincase breadth (BB) $<48\%$ of CBL · **S. megalura**
   Tail equal to or shorter than head and body, braincase broader, BB$>48\%$ of CBL · · 5

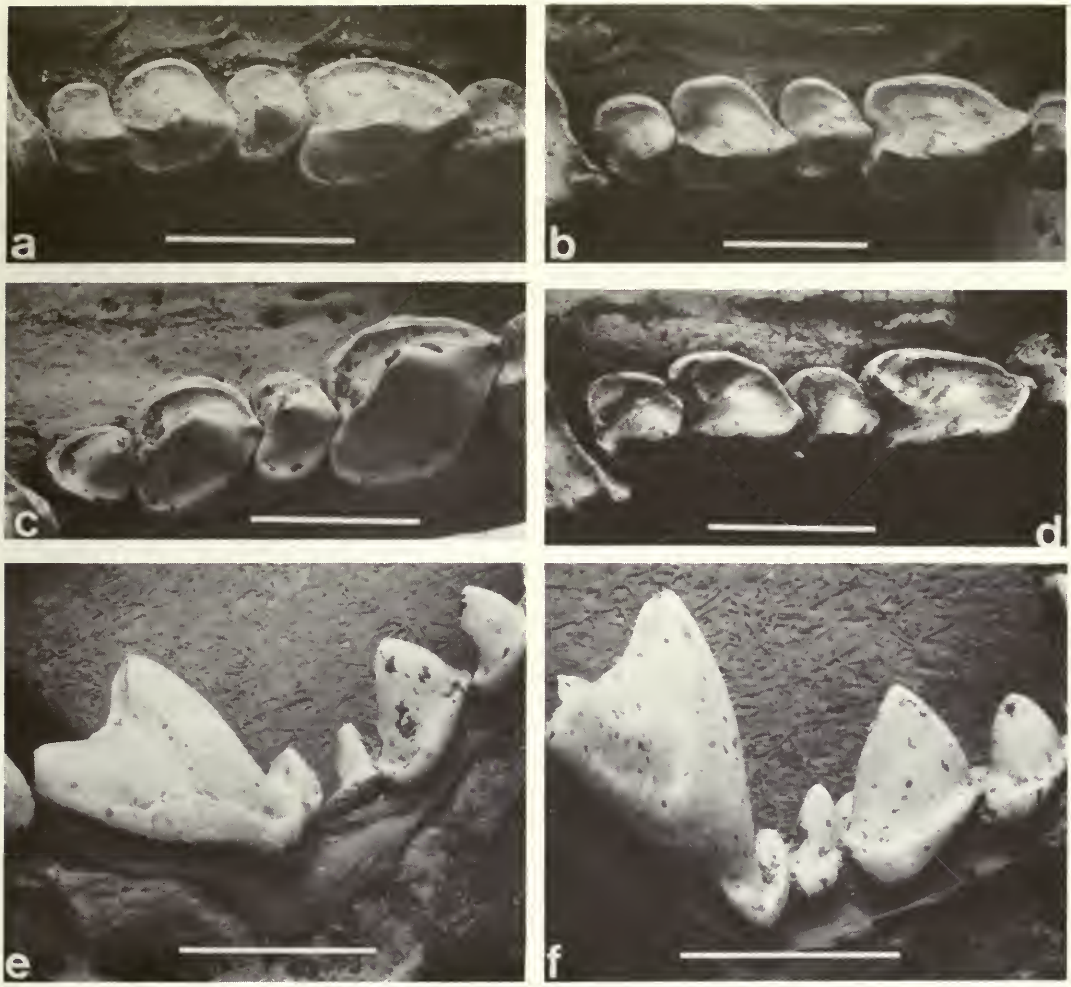

Fig. 6 (a-d) Crown view of left upper unicuspids: (a) *S. johnstoni*; (b) *S. howelli*; (c) *S. granti*; (d) *S. megalura*. (e-f) Labial view of left upper second, third and fourth unicuspids and premolar: (e) *S. granti*; (f) *S. howelli*. Scales 1 mm.

5. Small, CBL $<$ 15, UTL up to 6·5, M^3 anteroposteriorly compressed, $<$8% of UTL, talonid of M_3 reduced to a single cusp · **S. johnstoni**
Larger, CBL $>$ 15, UTL $>$ 6·5, M^3 not anteroposteriorly compressed, $>$8% of UTL, talonid of M_3 less reduced · 6
6. Tail lacking bristle-hairs, braincase deep, braincase height (BH) 4·5–5·0, $>$27% of CBL, talonid of M_3 similar to that of M_2 **S. granti**
Tail with bristle-hairs, braincase shallow, BH 4·1, $<$27% of CBL, talonid of M_3 reduced but talonid basin and entoconid ridge present. · · · · · · · · · · · · **S. howelli**

S. howelli is intermediate in size between the smaller *S. johnstoni* and the slightly larger *S. granti* but smaller than all other members of the genus (Table 1 & Figs 2–5). *S. morio* (Gray, 1862) *S. lunaris* Thomas, 1906 and *S. ollula* Thomas, 1913 are readily distinguished from *S. howelli* by their much greater size and require no further detailed comments; their measurements are included in table 1 for comparative purposes.

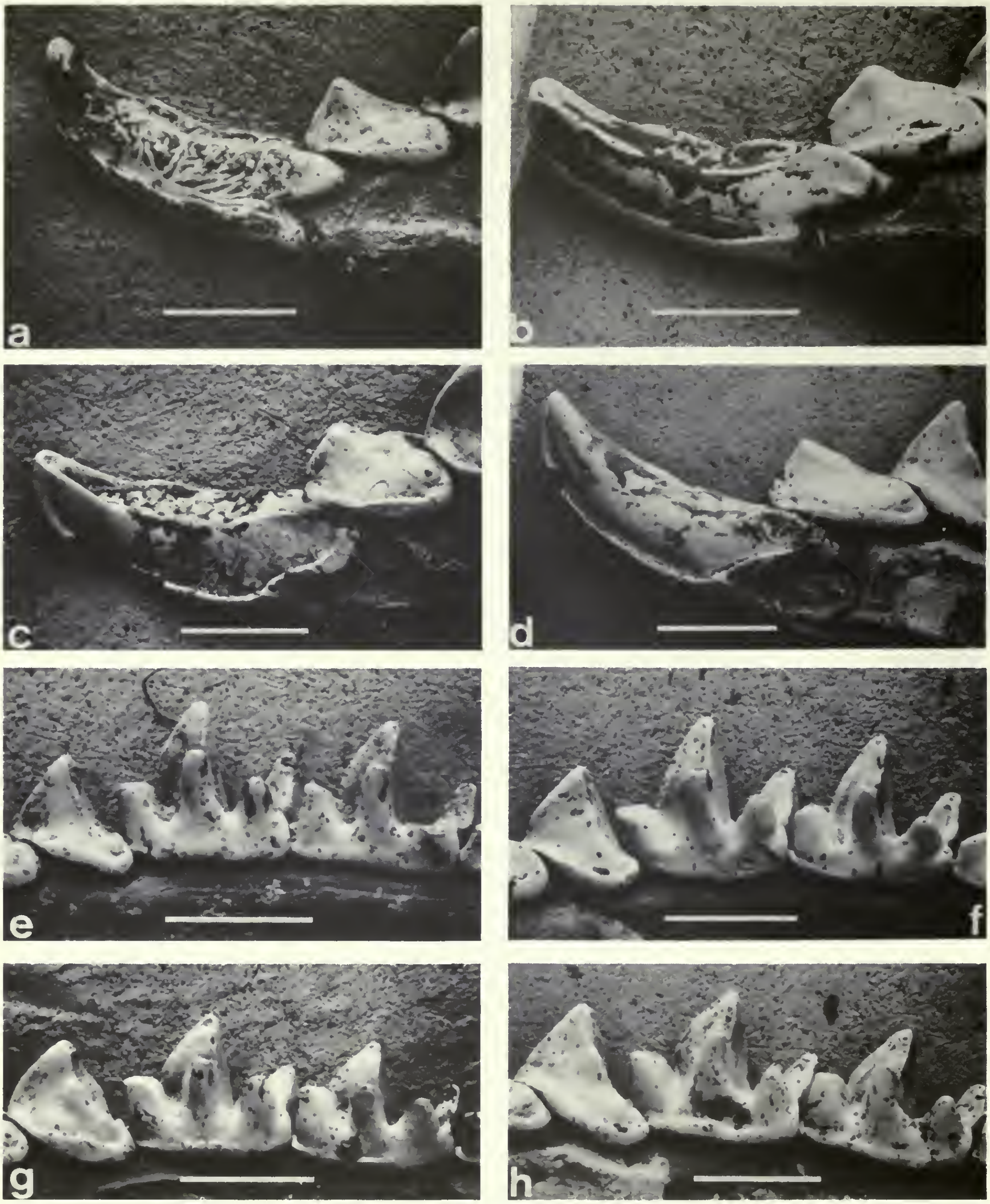

Fig. 7 (a-d) Lingual view of right lower first and second incisors. (e–h) Lingual view of right lower premolar and first and second molars. (a & e) *S. johnstoni*; (b & f) *S. howelli*; (c & g) *S. granti*; (d & h) *S. megalura*. Scales 1 mm.

The skull of *S. howelli* has a moderately broad, shallow, long braincase relative to skull length, in comparison with other members of the genus (Table 2 & Figs 2–4). *S. johnstoni* has a broad, moderately deep and long braincase; *S. granti* has a broad, deep, moderately long braincase and *S. megalura* a narrow, moderately deep and long braincase.

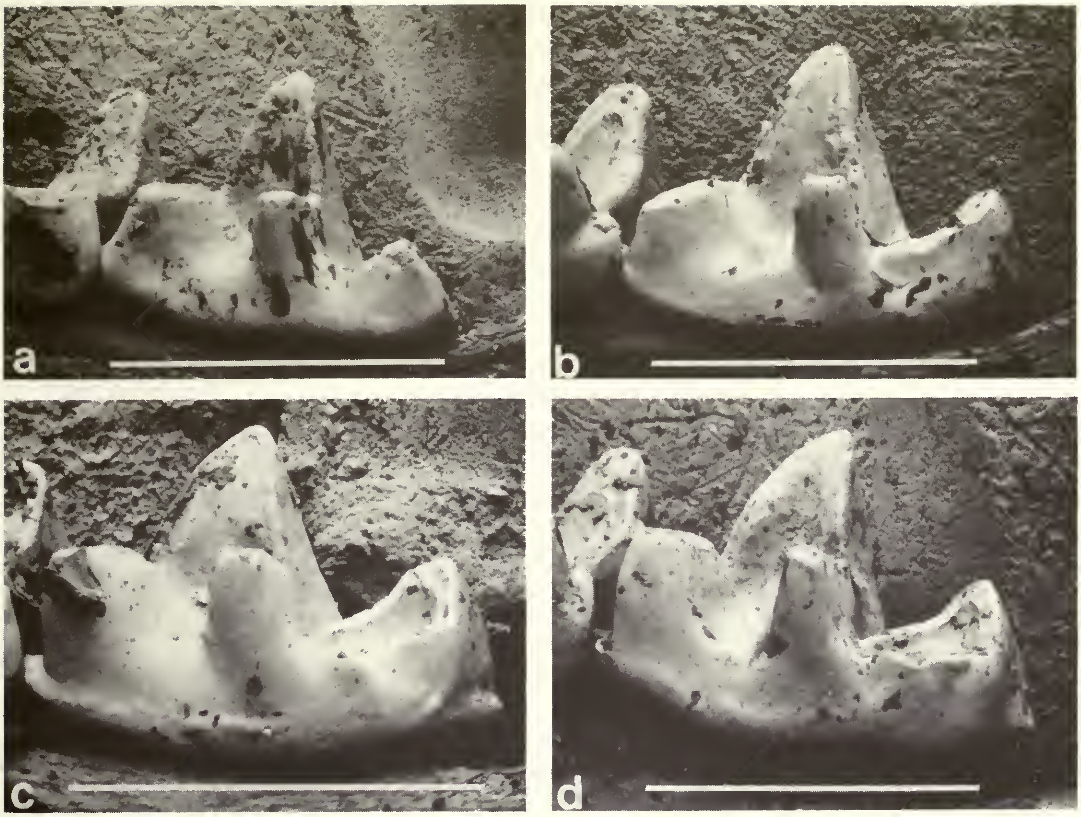

Fig. 8 Lingual view of right lower third molar: (a) *S. johnstoni*; (b) *S. howelli*; (c) *S. granti*; (d) *S. megalura*. Scales 1 mm.

The ascending ramus of the mandible is rather short and broad in *S. howelli* (Fig. 5). The ramus in *S. johnstoni* is high and narrow. Height of the ascending ramus at the coronoid process is less in *S. howelli* than in *S. granti* or *S. megalura* (Table 1).

The dentition of *S. howelli* is distinctive (see description). The main differences between the four species are illustrated in figures 6–8 and discussed below. The degree of development of the lingual cingulum on the upper unicuspids varies from broad in *S. johnstoni* and *S. granti* to very broad in *S. megalura* and *S. howelli* (Fig. 6). In *S. howelli* the lingual edge of the second upper unicuspid projects beyond that of the first and is level with that of the third, while in the other three species the lingual edge of the second upper unicuspid does not project as far as that of the first and third unicuspid.

The parastyle of the upper premolar is low and slender in *S. howelli* but medium in height and well developed in the other three species. *S. granti* is illustrated as an example of the condition in all three species in comparison with *S. howelli* (Fig. 6).

The third upper molar is a large tooth in *S. granti* and *S. megalura*, it is somewhat smaller in *S. howelli* but is anteroposteriorly compressed in *S. johntoni* (Table 1).

The posterolingual ridge of the first lower incisor (I_1) is higher than the posterior ridge and forms a small cusp in *S. howelli*, unlike the condition in the other three species (Fig. 7). The anterolingual ridge of I_1 does not extend onto the lateral enamel extension and a posterolingual cingulum is absent in *S. johnstoni* and *S. howelli*. In *S. granti* and *S. megalura* there is a well developed anterolingual ridge, extending onto the lateral enamel extension to form a posterolingual cingulum.

Table 1

		S. johnstoni	*S. howelli*	*S. granti*	*S. megalura*	*S. morio*	*S. lunaris*	*S. ollula*
Condylobasal length		13·9–14·5	15·9	15·8–16·9	16·4–17·6	18·2–18·8	20·9–21·8	23·5–24·0
	x̄	14·21		16·41	17·06	18·43	21·35	23·75
	n	7	1	11	9	3	2	2
Upper toothrow length		6·1–6·5	7·0	6·7–7·3	7·2–7·6	8·3–8·4	9·5–9·8	10·5
	x̄	6·35		7·07	7·38	8·34	9·67	
	n	6	1	9	9	3	3	1
Maxillary breadth at level of M²		4·45–4·7	4·7	4·7–5·3	4·7–5·2	5·2–5·4	5·7–6·1	6·8–7·1
	x̄	4·59		4·90	5·00	5·30	5·90	6·95
	n	7	1	11	9	3	3	2
Least interorbital breadth		3·35–3·6	3·7	3·8–4·3	3·7–4·0	4·3–4·6	4·4–4·6	4·9–5·3
	x̄	3·46		3·98	3·86	4·43	4·50	5·10
	n	7	1	11	9	3	3	2
Length of mandible		7·49–7·9	8·0	7·8–8·9	8·6–9·1	9·8–10·35	10·7–11·6	13·1–13·7
	x̄	7·66		8·45	8·79	10·08	11·13	13·40
	n	7	1	11	9	3	3	2
Height of ascending ramus of mandible at coronoid process		3·5–3·7	3·6	3·7–4·0	3·9–4·3	4·2–4·4	4·9–4·5	5·9–6·5
	x̄	3·6		3·87	4·03	4·30	5·20	6·20
	n	7	1	11	9	3	3	2
Length of M³ as a % of upper toothrow length		7·49–7·9	8·6	9·0–9·7	8·8–9·7	9·0–9·6	6·8–7·2	5·7
	x̄	7·74		9·37	9·26	9·40	7·07	
	n	6	1	9	9	3	3	1

x̄ = mean; n = sample size.

Table 2

		S. johnstoni	S. howelli	S. granti	S. megalura
Braincase breadth		7·0–7·5	7·7	8·0–8·6	7·6–8·1
	$\bar{x}$	7·30		8·28	7·84
	n	7	1	11	9
Braincase height		3·8–4·0	4·1	4·5–5·0	4·4–4·7
	$\bar{x}$	3·87		4·75	4·55
	n	7	1	11	9
Braincase length		5·6–5·8	6·8	6·6–7·1	6·8–7·4
	$\bar{x}$	5·73		6·85	7·11
	n	7	1	11	9
Braincase breadth as		49·0–54·0	48·4	49·1–51·9	43·7–47·6
a % of condylobasal	$\bar{x}$	51·38		50·48	46·01
length	n	7	1	11	9
Braincase height as		26·6–28·1	25·8	27·5–30·9	25·9–28·3
a % of condylobasal	$\bar{x}$	27·24		28·92	26·69
length	n	7	1	11	9
Braincase length as		39·6–41·1	42·8	40·7–42·6	40·8–42·0
a % of condylobasal	$\bar{x}$	40·31		41·72	41·70
length	n	7	1	11	9

$\bar{x}$ = mean; n = sample size.

A posterolingual ridge is present on the second lower incisor of *S. howelli*, it is weakly developed in *S. granti* and *S. megalura* but absent from *S. johnstoni* (Fig. 7).

There is no protostylid and a metaconid is barely indicated on the lower premolar of *S. howelli;* both protostylid and metaconid are lacking in *S. johnstoni;* both protostylid and metaconid are present in *S. granti,* while a metaconid only is present in *S. megalura* (Fig. 7). In all three species except *S. howelli,* a small cusplet is present in the posterior part of the valley between the posterior ridge and the posterolingual ridge.

The talonid of the third lower molar is reduced to a single cusp, the hypoconid, in *S. johnstoni* (Fig. 8). It is reduced to a small talonid basin and an entoconid ridge in *S. howelli.* In *S. granti* and *S. megalura* less reduction has occurred and the talonid resembles that of the second lower molar.

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A new species of the *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from Thailand

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While Curator of Terrestrial Vertebrates at the Thai National Reference Collection (now a part of the Thailand Institute of Scientific and Technological Research) the late Kitti Thonglongya undertook a survey of the bats of Thailand and their associated parasites, collecting extensively throughout the country. For the most part the bats that he collected were reported on the basis of a broad sample by Hill (1975). Those sent to London for examination included an example of *Hipposideros* from Rat Buri (TNRC 54-2080, now BM(NH) 78.2344) initially referred to *H. ater* Templeton, 1848 but which proved to differ quite clearly either from this species or from *H. cineraceus* Blyth, 1853 which in some superficial respects it resembled. No further study was undertaken at the time, Hill (1975) listing it as *Hipposideros* sp. but noting that it could not be referred to *ater* or to *cineraceus* from which it differed in certain features of the noseleaf and skull, or in size. Further similar specimens have now been found in the Thai National Reference Collection and more detailed study has established that all represent an undescribed species: additionally, another example in London (BM(NH) 78.2346, formerly TNRC 54–1961) proves also to represent the new species, rather than *H. cineraceus* as was thought originally.

Hipposideros halophyllus sp. nov

Hipposideros sp.: Hill, 1975: 27, Rat Buri, Thailand.
Hipposideros cineraceus: Hill, 1975: 29 (in part), Phet Buri, Thailand; Lekagul & McNeely, 1977: 165 (in part), fig. 61.

HOLOTYPE. ♂ TNRC 54–3694. Khao Sa Moa Khon, Tha Woong, Lop Buri, Thailand. Collected by Kitti Thonglongya. In alcohol, skull extracted, rear of cranium slightly damaged.

OTHER MATERIAL EXAMINED IN LONDON. ♂♂, ♀ TNRC 54–3696, 54–3697, 54–3705. All from the type locality. In alcohol, skulls extracted.

♂ BM(NH) 78.2344. Tham Khao Bin, Rat Buri, Thailand. Originally TNRC 54–2080. In alcohol, skull extracted.

♂ BM(NH) 78.2346. Tham Khao Yoi, Phet Buri, Thailand. Originally TNRC 54–1961. Skin and skull.

OTHER MATERIAL EXAMINED IN BANGKOK. ♂♂ TNRC 54–3695, 54–3706, ♀♀ TNRC 54–3704, 54–3710. All from the type locality. In alcohol, skulls of TNRC 54–3695, 54–3710 extracted.

DIAGNOSIS. A member of the *bicolor* group (Hill, 1963) of *Hipposideros*, characterized externally by large rounded ears lacking any sharply defined point or any definite fold or thickening at the antitragal lobe; by the absence of lateral supplementary leaflets beneath the antero-lateral margin of the anterior leaf, which has a shallow median emargination, and by the expansion of the internarial septum to form a small, disc-like structure just anterior

Bull. Br. Mus. nat. Hist. (Zool.) **47**(1): 77–82 Issued 28 June 1984

to the nostrils. The skull is elongate and narrow, the zygomatic width less than the mastoid width, the braincase moderately inflated anteriorly, with a low, narrow rostrum, broad basisphenoid depression and wide basioccipital, the tympanic bullae long and narrow and the inflated part of the cochleae elongate rather than subcircular. The new species is similar in size and ear structure to *Hipposideros cineraceus* or to *H. ater* but may be distinguished by its internarial structure and elongate tympanic bullae. Among other Asian species it has some resemblance to *H. ridleyi* in the disc-like expansion of the internarial septum but *ridleyi* is much larger (length of forearm c. 48 mm) and its internarial disc is relatively much larger, thinner and more saucer-like.

DESCRIPTION. Small (length of forearm 35·1–38·2 mm). Ears large, broad and rounded with broad, poorly defined tip, the anterior margin strongly convex, lacking any basal lobe, the posterior margin of the ear slightly convex for much of its length, deflected sharply to a wide, anteriorly rectangular antitragal lobe; a very slight thickening of the integument of the ear at the rear of the antitragal lobe but no definite fold or obvious antitragal modification. Outer (medial) surface of conch haired for about one half or a little more the length of the ear, the hairs proximally rather dense and long, more distally sparser and shorter; a sparse scattering of short hairs along the anterior border of the inner surface of the conch.

Muzzle low, not especially broadened, with small, narrow noseleaf lacking lateral supplementary leaflets; anterior leaf narrow, rather elongate, its total width about two thirds of the width of the muzzle, widest at a point level with the nostrils, narrowed anteriorly with a small, rounded median emargination. Central part of internarial septum expanded into a small, rounded, lobular and thickened disc-like structure lying in the narial depression slightly anteriorly to the nostrils: laterally this disc is slightly swollen, with a shallow median trough separating its lateral lobes; anteriorly the margins of the expansion curve sharply inwards to join the anterior leaf by a short, constricted and unthickened internarial segment, posteriorly merging similarly but less abruptly with the base of the intermediate leaf. Narial lappets small but evident, the nostrils very slightly pocketed. Intermediate leaf sometimes with four small glands, not sharply demarcated from anterior leaf and not especially elevated or inflated. Posterior leaf high, slightly semicircular, its lower half or a little more divided by three broad, ill-defined septa into four shallow pockets, its upper part smooth; no serrated structure on its posterior face. A prominent frontal sac with horizontal aperture lies immediately behind the posterior leaf in male examples, represented in a female specimen by a small tuft of hair.

All but one of the specimens available in London are in alcohol and have been so for some years: the sole dry example also appears to have been preserved in this way, possibly for a considerable period. The dorsal surface is now mid-brown, the hairs pale cream at the base and generously tipped with the brown terminal colour, which doubtless has been bleached to some extent by fluid preservation; the ventral surface is paler, largely lacking any brown, and has a greyish or greyish buff tinge.

Skull very small (condylocanine length 12·7–13·1 mm) with inflated, elongate and rather narrow braincase, its length from occiput to narrowest part of postorbital constriction one fifth greater than its greatest width across the mastoids. Postorbital region strongly constricted, the rostrum narrow and uninflated, its greatest supraorbital width about two fifths of the mastoid width; anterior and lateral rostral compartments not much inflated, the anterior part of the rostrum in profile a little below rather than level with the junction of the sagittal and supraorbital crests, the upper profile of the rostrum sloping slightly downward anteriorly rather than horizontal, and curving smoothly rather than abruptly to the maxillae. Zygomata robust, with a low jugal eminence; anteorbital foramen elongate, closed by a narrow bar of bone. Premaxillae making a broadly V-shaped junction with the maxillae; palate long, narrow, the toothrows strongly convergent anteriorly; palation rounded, level anteriorly with a line joining the anterior faces of m^{3-3}. Mesopterygoid fossa wide, the pterygoids slightly flared; sphenoidal bridge moderate, flanked by elongate apertures; basisphenoidal depression wide and shallow, subcircular in outline; basioccipital wide, the cochleae widely separated. Tympanic bullae long, narrow, almost platelet-like, anteriorly approaching the rear of the glenoid fossa, in length considerably exceeding the antero-posterior diameter of the exposed part of the associated cochleae, while in width the tympanic bullae are equal to rather less than one half the diameter of the exposed part of the associated cochleae along the other axis; cochleae small, not much inflated, their greatest exposed width about one and three quarter times their distance apart, the exposed part more elliptical rather than subcircular in outline.

Dentition with no unusual features; upper incisors weak, their tips convergent, the outer lobe obsolescent; anterior upper premolar (pm^2) small, compressed between the canine and the second upper premolar (pm^4) or very slightly extruded but nonetheless separating these teeth; posterior ridge of last upper molar one half of the length of its anterior ridge; outer lower incisors rather larger in crown area than inner lower incisors; anterior lower premolar (pm$_2$) about equal in length to second lower premolar (pm$_4$) and one half to three quarters its height.

Measurements of the holotype, followed by minima and maxima of the series of six (except where indicated in parentheses) measured in London: length of forearm 37·1, 35·1–38·2; condylocanine length 12·7, 12·7–13·1 (5); least interorbital width 2·0, 2·0–2·1; rostral width 3·6, 3·6–3·7; width across anteorbital foramina, 3·6, 3·5–3·7; zygomatic width 7·4, 7·2–7·4; width of braincase 6·9, 6·5–6·9 (5); mastoid width 7·8, 7·6–7·9, c^1–c^1 (alveoli) 3·1, 3·0–3·3; m^3–m^3 4·8, 4·8–4·9; width sphenoidal depression 2·7, 2·6–2·8 (5); width basioccipital 2·68, 2·62–2·77; c–m^3 4·8, 4·7–4·8; length complete mandible from condyles 8·5, 8·2–8·6 (5); length right ramus from condyle 8·9, 8·9–9·2 (4); c–m$_3$ 5·1, 5·0–5·2; length tympanic bulla 2·57, 2·49–2·72, width tympanic bulla 1·08, 0·98–1·13; antero-posterior diameter of cochlea 2·01, 1·80–2·03; transverse diameter of exposed part of cochlea 2·23, 2·21–2·33.

ETYMOLOGY. The name of the new species is drawn from αλωs, a disc, and øύλλov, a leaf.

REMARKS. The noseleaf of this new species is described (p. 165) and illustrated (fig. 61) by Lekagul & McNeely (1977) as *Hipposideros cineraceus.* The illustration of the skull (p. 166) of *H. cineraceus* provided by these authors is in fact of that species, having in contrast to the skull of *H. halophyllus* an inflated, higher rostrum, broad, short tympanic bullae and rounded rather than elongate cochleae. The material of *H. halophyllus* examined in London has come from the Thai National Reference Collection: all but one of these specimens was identified initially as *H. cineraceus* in Thailand, the exception being referred formerly to *H. ater.* Evidently Lekagul & McNeely employed a specimen labelled *H. cineraceus* from this collection as the basis of their description and illustration of the noseleaf.

The new species is similar in size to *Hipposideros cineraceus* and a little smaller than *H. ater,* with either of which it can at first inspection be confused. Its ears are similar in size and shape to those of *cineraceus* but in this species there is a distinct fold or thickening at the antitragal lobe. There is also a slight thickening with a small antitragal fold in the ear of *H. ater*. The anterior leaf in *H. halophyllus* is shallowly but distinctly emarginated just above the centre of the upper lip: neither *cineraceus* nor *ater* display any such emargination and although in both of these the internarial septum is inflated and sometimes bulbous there is no evidence of the development of any disc-like structure between and slightly in advance of the nostrils, the septum remaining more or less parallel-sided although swollen. Cranially, *halophyllus* may be distinguished from *cineraceus* and *ater* by its less inflated anterior narial compartments and lower anterior rostrum which slopes more gently to the canines, by its narrower, longer tympanic bullae, its more elongate rather than subcircular cochleae, and by its broader basioccipital.

DISCUSSION. Modification of the internarial septum into a circular or subcircular disc in *Hipposideros* occurs in the three African species *H. curtus* Allen, 1921, *H. jonesi* Hayman, 1947 and *H. marisae* Aellen, 1954, and also in one other Asian species, *H. ridleyi* Robinson & Kloss, 1911 from Malaya and Borneo. All belong to the *bicolor* group of *Hipposideros* and except for *curtus* are allocated by Hill (1963) to the *bicolor* subgroup, characterized by

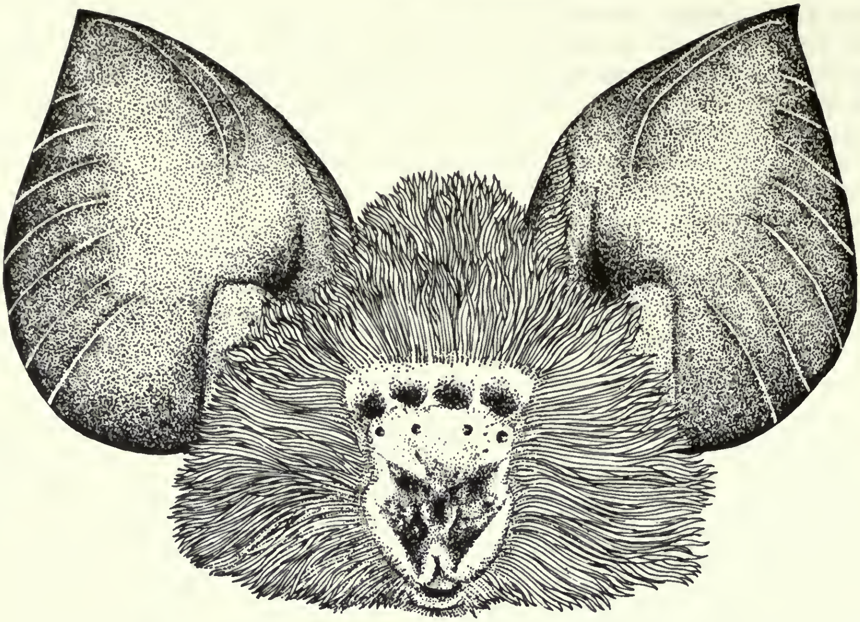

Fig. 1. *Hipposideros halophyllus.* ♀ TNRC 54–3704. Head × 5

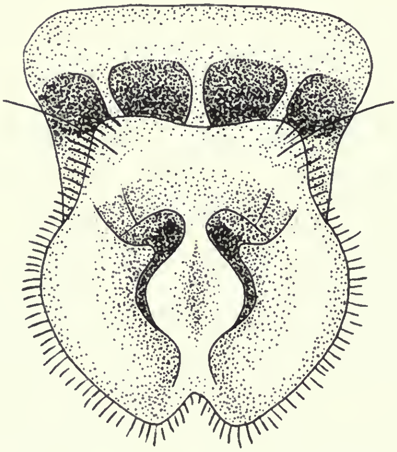

Fig. 2 *Hipposideros halophyllus.* ♂ BM(NH) 78.2344. Noseleaf × 10

broad, rounded ears with an internal fold or thickening at the antitragal lobe and haired for one half or less of their length, by the absence of lateral supplementary leaflets or by the presence of no more than a single small leaflet, and by an elongate and narrow skull with an inflated braincase, the zygomatic width rarely exceeding the mastoid width. Although in *curtus* the ears are broad, rounded and haired for only one half of their length, this species has two supplementary leaflets and cranially approaches the *galeritus* subgroup to which Hill (1963) allocated it. The members of this subgroup are more usually characterized by their generally more triangular ears which often have a concavity in the posterior margin just below the tip, a less prominent antitragal fold and are pilose externally for about two

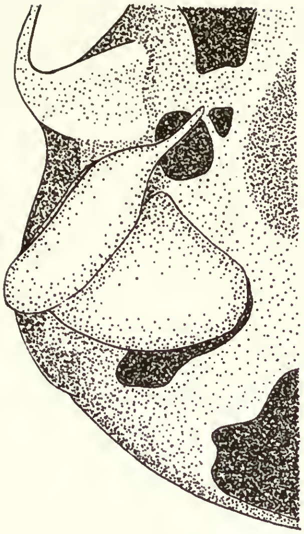

Fig. 3 *Hipposideros halophyllus.* ♂ BM(NH) 78.2346. Auditory region of skull × 10

thirds of their length, by the presence of two or three supplementary leaflets, and by a shorter, broader skull.

In size *Hipposideros halophyllus* is similar to *marisae* but the ears of this species although having little or no antitragal folding or swelling are rather more triangular in outline, like those of *jonesi* or *ridleyi*, and have a more clearly defined tip. There is one small lateral supplementary leaflet in *marisae*: *ridleyi* like *halophyllus* effectively lacks supplementary leaflets while in *curtus* the single leaflet extends forward beneath the anterior leaf to the median line. The internarial structure of *halophyllus* resembles that of *marisae* or *curtus*: in all the disc-like expansion is more or less lobulated, in *curtus* extending a little further posteriorly between the nostrils which however it does not greatly conceal. The internarial expansion in these species differs quite markedly from the circular internarial disc found in *jonesi* and *ridleyi* which is relatively larger, flatter, thinner and more saucer-like and which at least to some extent conceals the nostrils. The structure of the posterior leaf in *halophyllus* also resembles that of *marisae* or *curtus* but the septa supporting its lower part are broader and less well defined and the pockets that they delimit are shallower. In *jonesi* and *ridleyi* the posterior leaf is very high and it is clearly demarcated into four deep pockets in its lower part. Although in ear and noseleaf structure *halophyllus* has a number of features in common with *marisae,* the rostrum of the latter is not especially low, its tympanic bullae are not narrow and elongate and its cochleae are rounded: they are, however, separated by a wide basioccipital as in *halophyllus.*

Affinities and relationships in the *bicolor* group of *Hipposideros* were discussed in some detail by Hill (1963) who pointed out that a number of its species linked the two loosely defined subgroups into which he divided it. Among these *Hipposideros marisae* has features that are chiefly those of the *bicolor* subgroup but has ears that tend towards the *galeritus* subgroup, while *curtus* to some extent displays the opposite combination. It is also interesting that similar, indeed parallel developments in the structure of the internarial septum have occurred in the group in both Asia and Africa. In both regions the group has produced species (*halophyllus, marisae, curtus*) with a swollen, more or less disc-like structure closely associated with the nostrils. At the same time, each region has a further species (*ridleyi, jonesi*) with this expansion apparently carried further to produce a larger, thinner disc that covers much of the narial depression and partially obscures the nostrils, which are deeply pocketed.

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British Museum (Natural History)

Tilapine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

The tilapias are cichlid fishes of Africa and the Levant that have become the subjects of fish-farming throughout the warm countries of the world. This book described 41 recognized species in which one or both parents carry the eggs and embryos in the mouth for safety. Substrate-spawning species, of the now restricted genus *Tilapia*, are not treated here.

Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes
Part II: Phylogenetic analysis

Robert A. Travers

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Part II: Phylogenetic analysis

BRITISH MUSEUM
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NATURAL HISTORY

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Department of Zoology, British Museum (Natural History), Cromwell Road, London
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Synopsis

The Mastacembeloidei or spiny eels (comprising the families Mastacembelidae, Chaudhuriidae and Pillaiidae) is a distinctive group of about 70 freshwater species with a tropical and subtropical Oriental and Ethiopian distribution, currently recognised as a suborder of the perciform fishes. The majority of its 70 species have been placed in a single genus, *Mastacembelus*, without regard to their genealogical relationships, and the suborder as a whole has never been the subject of a detailed taxonomic or anatomical review. A revision of the genera and families within the suborder, and a reconsideration of its interrelationships within the Percomorpha, are the overall objectives of this study.

It is based on numerous anatomical characters drawn from the descriptions in Travers (1984) and involves a comparison of their condition with that of their homologues in other teleostean lineages. This analysis indicates that the mastacembeloids, long associated with the Perciformes, should be reallocated to the Synbranchiformes. A phylogenetic hypothesis of their intrarelationships is also proposed, *viz.*, the Mastacembeloidei can be resolved into two lineages: the Chaudhuriidae (expanded to incorporate two genera) and the Mastacembelidae (divided into two subfamilies representing the Asian and African species). This hypothesis results in the elevation of the sole endemic Chinese species, *Mastacembelus sinensis*, to a monotypic genus within the Chaudhuriidae, and the generic synonymy of *Pillaia* (and *Garo*) with *Chaudhuria* (but the retention of both the latter taxa as subgenera of *Chaudhuria*). The Asian mastacembelid subfamily, Mastacembelinae, retains the genera *Mastacembelus* and *Macrognathus* although the former is restricted to six species only, and the latter expanded to include eight species previously included in *Mastacembelus*. The African species are shown to be phyletically distinct and to warrant the creation of a new subfamily and new genera for two major African sublineages.

Introduction

The Mastacembeloidei, or spiny-eels, are a group of freshwater teleost fishes occurring in the Oriental and Ethiopian zoogeographical regions. The Oriental species are widely distributed in SE. Asia and extend from the eastern China seaboard, through the continental islands of Indonesia to the Middle East (Fig. 1). This pattern, together with their recent discovery in southern Iran (Coad, 1979), gives these fishes a continuous distribution throughout their Oriental range. The absence of mastacembeloids from the Arabian Peninsula, North Africa and the Horn of Africa, however, has resulted in the geographical isolation of the Oriental fauna from the Ethiopian species. These are restricted to tropical and subtropical waters of Central Africa; embracing the Nilo-Sudan, Upper and Lower Guinea, Zaire, East Coast and Zambezi ichthyofaunal provinces of Roberts (1975).

Mastacembeloids occur in a variety of freshwater habitats at high and low altitudes, and are common in riverine and lacustrine environments, streams and ponds (Job, 1941; Sufi, 1956; Matthes, 1962; Poll & Matthes, 1962; Skeleton, 1976).

At least four African species are cavernicoles (Poll, 1953, 1958, 1959 & 1973 and Roberts & Stewart, 1976) and show considerable atrophy of the eye tissues, an associated hypertrophy of the superficial parts of the *adductor mandibulae* musculature and even lack of pigment (Poll, 1973). A group of Asian mastacembeloid taxa exhibit an elaborate burrowing mechanism (Job, 1941; Sufi, 1956); however, this habit is not found in all species (Schofield, 1962).

Most mastacembeloids appear to be carnivores with a wide range of feeding strategies. Food organisms range from small zooplankton (Job, 1941; Sufi, 1956) through aquatic insect larvae and oligochaetes (Roberts, 1980) to other fishes (pers. obs.) including both eggs and fry (Hamid Khan, 1934) and even mastacembeloid species with a relatively small adult size (Staeck, 1976). To a large extent the prey species are related to the size and developmental stage of the predators.

Reproduction in the mastacembeloids is poorly known. There are brief descriptions of the spawning activity in a single species in captivity (Schoenebeck, 1955; Polder, 1963; Franke, 1965), artificially induced spawning (Kochetov, 1982) and the periodic occurrence of vast numbers of juveniles in Lake Tanganyika (Brichard, 1978), but reproductive behaviour in nature has never been observed.

Many mastacembeloids are thought to have some form of aerial respiration (Dobson, 1874; Day, 1877; Ghosh, 1933; Hora, 1935), although reports are contradictory and the presence of suprapharyngeal or swimbladder adaptations has never been shown. Whether survival in oxygen deficient waters is by some form of cutaneous respiration (Mittal & Datta Munshi, 1971), or by inanition with respiration at a standstill (Job, 1941), requires further research before an accurate assessment can be made.

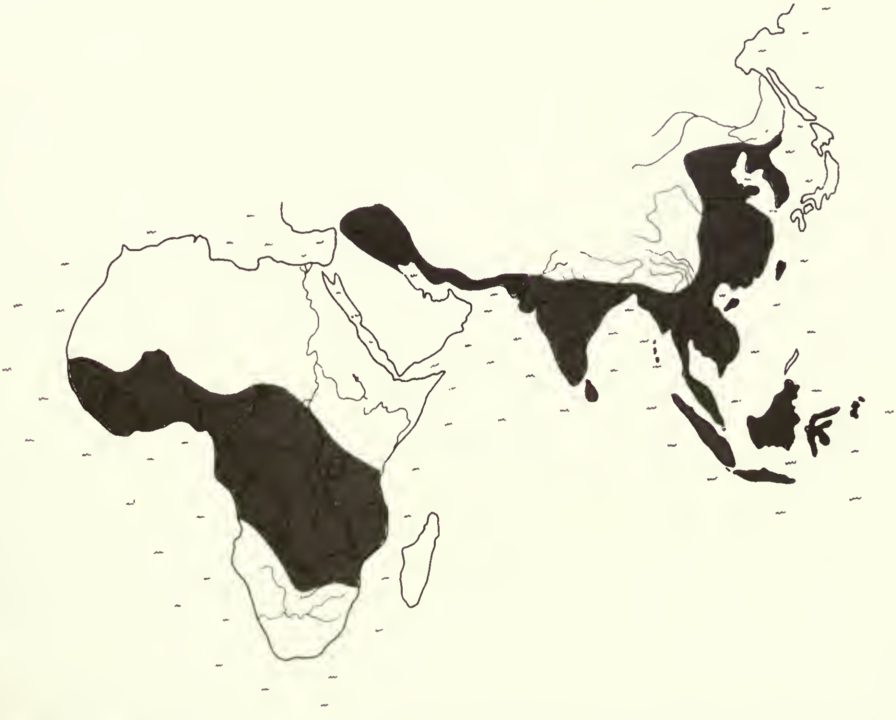

Fig. 1 Present-day distribution of mastacembeloid Oriental and Ethiopian species.

A pseudobranch, once thought to be absent in mastacembeloids (Day, 1889; Boulenger, 1915: 12) has recently been described in some Asian species (Bhargava, 1953). A spherical sac-like pseudobranch situated above the epithelium roofing the oral cavity was found in all taxa examined.

This study is based on the many osteological and myological features shown (Travers, 1984) to be of potential value in reconstructing phylogenetic relationships. These morphological characters will be analysed by comparing their condition with that of their homologues (Patterson, 1982*b*) in other groups of percomorph fishes (acanthomorphs) or with the teleosts as a whole (see below).

The objectives of these comparative studies, besides providing an analysis of mastacembeloid interrelationships with other percomorph fishes, was an attempt to revise the intrarelationships of the group. Only by revealing the phylogeny of these fishes can an improved understanding of their biogeographical history be gained (Greenwood, 1983).

Although numerous specific features were identified (see Travers, 1984), and are included where possible in the analysis, a formal species level revision was not attempted.

Materials and methods

Materials

The bulk of the comparative outgroup material examined is tabulated in Travers (1981). In addition to these specimens further taxa are listed in systematic order in Table 1; all are given with their register number and codes indicating the type of examination or preparation involved. Unless otherwise indicated, all are BM(NH) registered specimens.

For a complete list of the mastacembeloid specimens upon which this study is based, for nomenclatural references and the techniques of morphological analysis, see Travers, 1984.

Methods

The inter- and intrarelationships of the mastacembeloids were evaluated by the application of a cladistic methodology as originally defined by Hennig, 1950 & 1979 and advocated latterly by Eldredge & Cracraft, 1980, Nelson & Platnick, 1981, and Wiley, 1981. This methodology has, over the last decade, brought increased order to the complexities of teleostean classification regardless of the vociferous debate (e.g. see *Nature* Correspondence from volume **275** to **292**), and the proliferation of conceptual literature (e.g. see *Systematic Zoology* from 1967 (4): 289–292, to date), that it has engendered.

To determine the primitive (plesiomorphic) or derived (apomorphic) nature of mastacembeloid characters, in the absence of a complete ontogenetic history of all species, a series of outgroup comparisons was made in a manner similar to that discussed by Watrous & Wheeler (1981); see Farris (1982) for a critical review of their study. Information from ontogenetic transformations (de Beer, 1958; Gould, 1977; Nelson, 1978; Rosen, 1982), where available was utilized especially if comparisons could be made with similar developmental stages in outgroup taxa (Fink, 1982; Patterson, 1983).

Only those uniquely derived features confined to individuals of a single species were identified as autapomorphic characters. When detected in this restricted sense these characters can be used to identify species, regardless of whether or not they are strictly definable (Patterson, 1982*a*).

Where an outgroup has been the subject of a recent study, highly derived species were excluded so as not to be mislead by taxa that are unrepresentative for their group as a whole. In poorly studied assemblages a wide range of representatives was examined in order to avoid overlooking a group which may be masked by a previous incorrect assessment of its characters and hence given an erroneous taxonomic allocation.

Outgroup taxa were taken from all major percomorph assemblages. Emphasis was given to perciform lineages, since these represent the largest acanthopterygian groups, and several beryciform families since the perciforms are generally thought to have been derived from a beryciform species (Patterson 1964; Greenwood *et al,* 1966; McAllister, 1968; Zehren, 1979). However, these beryciform taxa are ill-defined and thought by most authors to represent polyphyletic assemblages (Patterson, 1964; Greenwood *et al,* 1966; Rosen, 1973; Zehren, 1979). Furthermore, the task of analysing such groups is complicated by the large number of taxa involved and also, as Rosen (1973: 398) observed, by: '. . . the lack of co-ordinated comprehensive studies of character complexes throughout the group'. For example, the only synapomorphy so far proposed for the Perciformes is the presence of an interarcual cartilage (Rosen & Greenwood, 1976) and even this has been shown recently to have a far wider occurrence than had been previously thought (Travers, 1981; it may even occur in some ophichthid eels (McCosker, 1977 and M. Leiby pers. comm.).

Table 1 Teleostean outgroup taxa (supplementary to those listed in Travers 1981).

Species	Reg. No.	Preparation
Arapaima gigas	Unreg.	DS
Elops hawaiensis	1962.4.3: 1–25	A
Elops machnata	1962.8.28: 1–7	A
Halosaurus owenii	1890.6.16: 55	AP
Notacanthus bonapartei	1972.1.26: 33–39	MD
Notacanthus sexspinis	1873.12.13: 27	DS
Anguilla anguilla	1962.6.5: 2–4	MD
Etrumeus teres	1923.2.26: 73–78	A
Ostichthys parvidens	1974.5.25: 747–753	MD
Holocentrus rufus	1976.7.14: 79–81	MD
Zeus faber	1971.7.21: 86–90	MD
Hypoptychus dybowskii	1979.11.26: 1–3	MD
Macrotrema caligans	1860.3.19: 943 Type	AP
Macrotrema caligans	1908.7.13: 1	AP
Monopterus cuchia	Unreg.	DS
Synbranchus bengalensis	1860.3.19: 1477	MD
Synbranchus javanicus	1862.11.1: 138	MD
Synbranchus marmoratus	1981.1.15: 1117–1119	MD
Mugil cephalus	1913.7.10: 31–34	MD
Pholis gunnellus	1981.2.20: 446–479	MD
Pholidichthys leucotaenia	1974.3.14: 1	MD
Pholidichthys leucotaenia	USNM 206237	A
Pholidichthys leucotaenia	USNM Gift	AP
Scytalina cerdale	USNM 70801	AP
Notograptus guttatus	USNM Gift	A/A
Ptilichthys goodei	USNM 130266	AP
Stichaeus (Leptoblennius) mackayi	1896.7.23: 183	MD

Abbreviations

Anatomical

Aa	Anguloarticular
Add Mand	*Adductor mandibulae*
Asph	Autosphenotic
Bbl 1–3	Basibranchial 1–3
Bbl KC	Basibranchial I keel cartilaginous
Bh	Basihyal
Bh + Bbl	Basihyal fused with basibranchial I
BR	Branchiostegal rays
Bs	Basisphenoid
C	Cleithrum

Com	Coronomeckelian
DO	*Dilatator operculi*
Dsph	Dermosphenotic
Ect	Ectopterygoid
End	Endopterygoid
F	Frontal
Fa	Fimbria
FDL	Frontal descending lamina
FFac	Frontal facet
Fu	Fimbrule
Hb 2–3	Hyobranchial 2–3
Hb3 AP	Hyobranchial 3 anterior process
Hyo	Hyomandibula
Hyo Add	*Hyohyoidei adductores*
HyoMF	Hyomandibula metapterygoid flange
Hyo SP	Hyomandibula symplectic process
Iop	Interoperculum
LE	Lateral ethmoid
LE xsc	Lateral extrascapula
Lig	Ligament
LO	*Levator operculi*
MC	Meckel's cartilage
Met	Metapterygoid
MExsc	Medial extrascapula
MP	Maxillary process
Op	Operculum
P	Parasphenoid
Pal	Palatine
Palopt	Palatopterygoid
PalT	Palatine teeth
PAW	Parasphenoid ascending 'wing'
Pop	Preoperculum
Pr	Prootic
PrAP	Prootic anterior process
Pt	Pterosphenoid
Ptm	Posttemporal
PtmT	Posttemporal tubule
Q	Quadrate
Ra	Retroarticular
Sc	Supracleithrum
Sen Pap	Sensory papillae
Sep	Septum (ossified)
Sop	Suboperculum
Sph	Sphenotic
Sym	Symplectic
Uh	Urohyal
UhAP	Urohyal ascending process

Note on the figures: even stipple-dots indicate the presence of cartilage. The scale on all figures indicates 1 mm.

Table of study material

A/A	Double stained transparency (alizarin red and alcian blue)
A	Alizarin stained transparency
DS	Dry skeleton preparation
MD	Muscle dissection (cheek & opercular region)
AP	Alcohol preserved specimen not available for dissection or preparation
Unreg.	Unregistered specimen held at BM(NH)

Institutional

BM(NH)	British Museum (Natural History).
USNM	United States National Museum, Washington.

Mastacembeloid interrelationships

I. Character analyses

Osteology

NEUROCRANIUM

The neurocranium exhibits the general trends (mainly reductional) and particular features that are currently recognised as diagnostic for acanthopterygian fishes (see Zehren, 1979: 163–166 for a recent summary), although they are somewhat masked by the extreme precommissural attentuation of the skull. Of the eleven acanthopterygian neurocranial and circumorbital character states listed by Patterson (1964: 449) and Zehren (*op. cit.*) eight are readily recognisable in almost all mastacembeloids. A further derived feature found by Patterson (1975: 568) only in the Acanthopterygii is the pons moultoni, a loop of bone on the inner face of the sphenotic which surrounds the anterior semi-circular canal.

The medial face of the sphenotic in mastacembeloids houses the anterior semi-circular canal in such a structure and thus conforms to the condition in the Acanthopterygii. Surprisingly, Zehren (1979) did not mention the pons moultoni in his study of the Beryciformes.

Elongation of the supraethmoid and vomer in mastacembeloids contributes to the generally pointed snout in these fishes, although the lateral ethmoids are of more usual proportions (Travers, 1984). In other percomorphs with elongate syncrania, including such forms as the congrogadids, pholidichthyids, sphyraenids, acanthurids, luciocephalids and synbranchids, the ethmovomerine region is not always attenuated. In *Congrogadus subduceus* and *Pholidichthys leucotaenia* this region is of similar proportions to that found in most other percomorphs, any elongation being restricted to the postorbital neurocranial bones. In *Sphyraena obtusata, Acanthurus bahianus* and *Luciocephalus pulcher* the ethmovomerine region is particularly elongated, whilst the braincase proportions are similar to those in most percomorph fishes. This condition is produced in *Sphyraena* by elongation of the lateral ethmoids, whilst in *Luciocephalus* the prevomer and nasals are particularly lengthened (Liem, 1967). The anterior region of the parasphenoid is particularly long in *Acanthurus* and, combined with the long supraethmoid, it contributes to the elongate ethmovomerine region.

The vomer in synbranchids was described by Rosen & Greenwood (1976: 49) as a ‘long, thin strut’ elongated to a point below the pterosphenoids and basisphenoid. This is the only outgroup examined which has a vomerine shaft comparable in length to that in the mastacembeloids (e.g. compare the vomerine length in Rosen & Greenwood, 1976, figs. 57 & 59 with the vomer in other percomorphs). This may well be a synapomorphy of these taxa.

Although an elongate ethmovomerine region occurs in a variety of what appear to be phyletically distant percomorph fishes, the method by which elongation is achieved in the mastacembeloids (by extreme lengthening of the vomer and supraethmoid) is not found in any other group (apart from a similar elongation of the vomer in the synbranchids).

The sensory canal bearing bones of the ethmovomerine region (i.e. the nasal and 1st infraorbital) are also elongated, and the nasal has a particularly broad dorsal surface in mastacembeloids.

The 1st infraorbital is long and tapered in a variety of percomorphs, including the synbranchids, ammodytids and luciocephalids. However, the nasal in these taxa is barely broader than the sensory canal it carries.

The concomitant elongation in the mastacembeloids of the supraethmoid, vomer and 1st infraorbital bone, accompanied by a long nasal with a broad dorsal surface, results in a snout unlike that found in any of the other taxa examined. It is thus considered to be a synapomorphy for the group.

The mastacembeloid lateral ethmoid is not elongate although the ‘ethmoids’ (presumably including the lateral ethmoid) were included by Rosen & Greenwood (1976) in their list of 'greatly attentuated' mastacembeloid neurocranial elements. In fact the lateral ethmoids retain the general percomorph proportions, but are fused in the midline and have an overall tubular shape.

In percomorph fishes the lateral ethmoids are generally plate-like bones lying on either side of the supraethmoid and are separated from each other medially by the cartilaginous, posteroventral end (septal cartilage) of the supraethmoid.

Medial fusion of the lateral ethmoids in mastacembeloids, dorsal to the cartilaginous posterior end of the supraethmoid is an arrangement found also in blennioids, (e.g. *Notograptus guttatus*) and in gobioids (e.g. *Trypauchen wakae*). However, the tubular shape of the lateral ethmoids was not found in any other outgroup taxa.

The mastacembeloid pterosphenoids have wide lateral faces and are connected ventromedially (Travers, 1984: 51).

Among the outgroups examined (see Table 1) medial pterosphenoid connections were found only in the clupeid *Etrumeus,* some beryciforms (e.g. *Diretmus argenteus* and *Ostichthys trachypoma*; Zehren, 1979) and the anabantoids (e.g. *Belontia* and *Trichogaster leeri*; Liem, 1963).

In the anabantoids the pterosphenoids are not connected ventrally, but dorsally are linked by long wing-like processes, running transversely across the orbital cavity. In two beryciform families (Diretmidae and Holocentridae) Zehren (1979: 232) found the pterosphenoids to have their '... anterior lower edges meet in the midline closing off the optic fenestra' and, on the basis of outgroup comparisons concluded that this arrangement represented the apomorphic condition (see below).

In synbranchids the massive development of the pterosphenoids has been noted by Rosen & Greenwood (1976: 44) who found that, with the basisphenoid, these bones occupy '... somewhat less than half the total length of the neurocranium'. Although the pterosphenoid is large in synbranchids it does not contact its partner in the midline. Rosen & Greenwood (1976) also listed the bones involved in the neurocranial lengthening of mastacembeloids, when comparing them with synbranchids, but failed to mention the central role of the pterosphenoids.

The wide lateral face of the pterosphenoids and their medial union ventrally (resulting in the ventral half of the optic foramen being bounded by them) is a synapomorphic character of all the mastacembeloids (its absence in *Pillaia* and *Mastacembelus aviceps* is discussed on p. 110). In the beryciforms in which the pterosphenoids are connected in the midline (discussed above), these bones lack wide lateral faces and their medial connection is thought to be convergent with that in the mastacembeloids.

The basisphenoid is a characteristically small, compressed bone in mastacembeloids (Travers 1984: 53). This configuration appears to be directly associated with the median pterosphenoid connection, and represents a derived state of the large Y-shaped bone present in most teleostean lineages. It can be noted that in beryciforms and *Etrumeus,* taxa also with medially fused pterosphenoids, the basisphenoid retains its plesiomorphic condition.

A preorbital (or, more correctly, suborbital) spine that pierces the skin is a characteristic feature of almost all mastacembeloids (Travers, 1984). A preorbital spine is also present in halosauroids (*sensu* Greenwood, 1977) as described by McDowell (1973) and illustrated by Greenwood (*op. cit.* figs. 5, 7, 9, 10 & 14), and in some Ostariophysii (e.g. Cobitidae). However, in these fishes it is produced, respectively, from the maxilla or the lateral ethmoid, and is not homologous with the mastacembeloid preorbital spine. Here the spine is the posterior end of the large first infraorbital bone. In no other teleostean taxon is the first infraorbital developed in this way, and the presence of the spine is a further valuable synapomorphy of the mastacembeloids.

A long prootic, characterised by a distinct anterior process passing across the anterolateral face of the neurocranium and into the orbital cavity, is typical of most mastacembeloid taxa (Travers, 1984: 58).

This is contrary to the opinion expressed by Springer & Freihofer (1976: 37) that, 'In the highly specialised Mastacembelidae and Chaudhuriidae the parasphenoid also lacks an ascending process but either the prootic is entirely blocked by the pterosphenoid-pleurosphenoid bones from entering the postorbital margin or the pterosphenoid-pleurosphenoid bones are absent (D. E. Rosen, pers. comm.)'.

The plesiomorph condition of the teleostean prootic is one in which the anterolateral edge contributes to the posterior rim of the orbit. In a few, and diverse, taxa the anterior margin of the prootic is prevented from bordering the orbit by the ascending parasphenoid process, the pterosphenoid and/or the descending lamina of the frontal. This occurs particularly in taxa with elongate neurocrania, and is seen in some *Lates* species illustrated by Greenwood (1976: fig. 3).

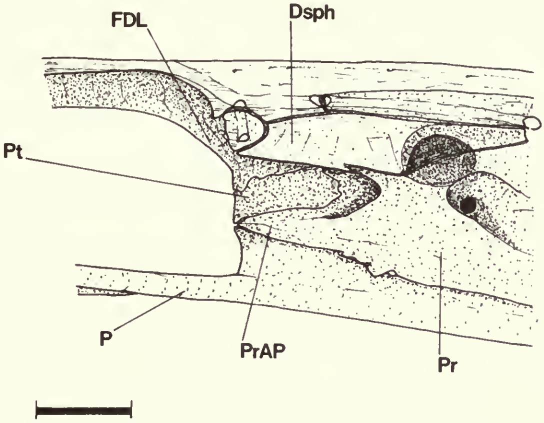

Fig. 2 *Congrogadus subduceus,* otic region of neurocranium; lateral view, left side.

A massive pterosphenoid and basisphenoid prevent the anterolateral extension of the prootic from entering the border of the small orbital cavity in the synbranchids (Rosen & Greenwood, 1976). In the Pholidichthyidae (Springer & Freihofer, 1976) the neurocranium is elongate and the prootic, lengthened anteriorly, has a wide lateral face, (Fig. 4a). The anterior region of the prootic in this taxon passess above the lateral face of the basisphenoid, and its anterior edge borders the posterior rim of the orbit. A very large prootic is also present in the congrogadids (e.g. *Congrogadus subduceus,* Fig. 2), and is distinguished by its long anterior region (between the ventral edge of the pterosphenoid and upper margin of the parasphenoid) which passes from the trigeminofacialis chamber to a point posterior to the rim of the orbit.

Thus, the large size of the prootic in mastacembeloids is not in itself exceptional. Rather, the exceptional feature is the anterior region of the prootic overlying the ventrolateral face of the pterosphenoid and being developed into a long anterior process extending into the orbital cavity. This constitutes a major synapomorphic feature of the mastacembeloid neurocranium.

The trigeminofacialis chamber lies in the prootic; its development has been discussed by Patterson (1964: 434–438). He concludes that the plesiomorphic condition for teleosts (as seen for example in *Elops*) was one in which the *truncus hyomandibularis,* the jugular vein and the orbital artery are separated by individual foramina in the pars jugularis. This condition differs from that in perciforms where the three foramina are confluent. The progressive reduction from four to two external openings in the pars jugularis among beryciform fishes has recently been demonstrated by Zehren (1979: 235) and lends support to Patterson's hypothesis (op. cit.) that '... during the evolution of teleosts there has been a simplification of the pars jugularis'.

A large trigeminal foramen (generally situated anterior to the lateral commissure) and a small facial foramen (generally medial to the lateral commissure) are the only foramina in the pars jugularis of mastacembeloids, which are apomorphic in this respect.

The mastacembeloid otic bulla is a small recess in the posteromedial face of the prootic, and completely houses the sacculus in most taxa. Only these fishes among the teleosts, have their saccular recess contained entirely within the prootic. In all others the recess is formed from the prootic, exoccipital and basioccipital. The relative contribution of these three bones does, however, vary from an almost equal contribution to one in which the greater part is derived from the prootic (e.g. congrogadids, tripterygiids of the genus *Paraclinus,* and *Channa obscura*).

This housing of the otolith bulla in the prootic only is a synapomorphic character of the mastacembeloids.

Precommissural elongation of the neurocranial bones in mastacembeloids involves that region of the autosphenotic lying anterodorsal to the lateral commissure (Travers, 1984: 69). This part of the sphenotic is produced into a wide anterolateral flange that generally extends across part of the lateral face of the pterosphenoid and descending frontal lamina, but does not enter the posterior border of the orbit. The postorbital process on the sphenotic, as a

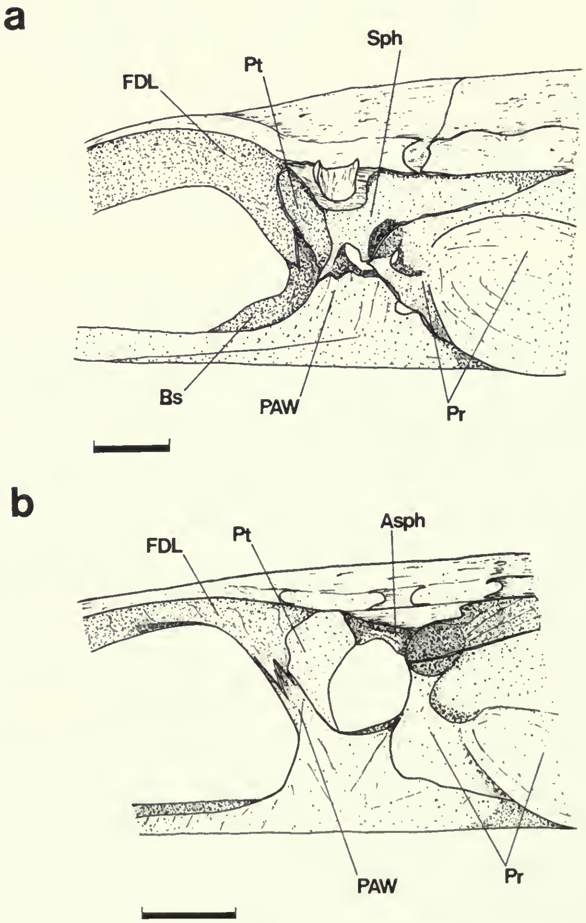

Fig. 3 Neurocranium of (a) *Ophidion rochei,* and (b) *Lycodes brevipes.* Left side of otic region, lateral aspect.

result of its anterolateral flange, has a posterior position relative to that of a similar process in other perciform fishes, for example the labroids (Rognes, 1973) and cichlids (Stiassny, 1981). This posterior position of the postorbital process indicates the extent to which the mastacembeloid sphenotic has expanded anteriorly.

In its plesiomorphic state the teleostean autosphenotic forms the posterodorsal corner of the orbit, a condition found in almost all major teleostean lineages, including many beryciform and perciform fishes.

Some development of the autosphenotic occurs in several phylogenetically distant acanthomorph lineages (e.g. *Ophidion rochei,* Fig. 3a; *Pholidichthys leucotaenia* and *Xiphistes mucosus,* Fig. 4a & b; *Ammodytes tobianus,* Fig. 4c), although in none is it developed to an extent comparable with that in the mastacembeloids, and in all the bone, unlike that in mastacembeloids, still forms the posterodorsal margin of the orbit. The ammodytoids, (e.g. *Ammodytes tobianus,* Fig. 4c) are the only other perciform group found to have a sphenotic with a wide anterolateral face. However, in these taxa the sphenotic forms the posterodorsal margin of the orbit and in this respect it retains the plesiomorph condition.

Thus, the condition of the wide anterolateral flange on the sphenotic in mastacembeloids which falls short of the postorbital margin, is a synapomorphy of the group.

The mastacembeloids lack a posttemporal fossa (Travers, 1984: 17). It is a common feature of lower teleosts and apart from having lost its bony roof, is widespread among higher euteleosts. In these fishes the posttemporal fossa generally lies lateral to the supratemporal fossa (Patterson, 1964: 449 & 1975: 392–5). Such fossae are typically found in the perciform neurocranium. The lack of a posttemporal fossa must, by virtue of the widescale presence of this fossa in teleosts, be a secondary loss and as such may be considered an apomorphic feature of these fishes. It is not, however, a feature restricted to these fishes. The fossa appears to have been lost independently in the following acanthomorph lineages: ophidioids (e.g. *Carapus acus*), synbranchoids (e.g. *Synbranchus marmoratus*), blennioids (e.g. *Notograptus guttatus*), trachinoids (e.g. *Trachinus vipera*) callionymoids (e.g. *Callionymus lyra*), acanthuroids (e.g. *Acanthurus bahrianus*) and channoids (e.g. *Channa obscura*).

A wide subtemporal recess in the posterolateral wall of the neurocranium, defined in part by the prootic, pterotic and exoccipital, is characteristic of all mastacembeloids (Travers, 1984) and is the site of origin for the levator musculature of the branchial arches. This recess, which is little more than a shallow lateral concavity, is not thought to be the homologue of the subtemporal fossa in lower teleosts (Forey, 1973; Patterson, 1975).

The occipital condyle in all mastacembeloid taxa is in the form of a tripartite, concave socket (Travers, 1984: 71) formed from equal contributions by the exoccipitals and the basioccipital. The hemispherical anterior face of the first centrum articulates in this socket.

A tripartite occipital condyle occurs in the majority of teleosts including the more basal assemblages (Forey, 1973: 12–19; Patterson, 1975: 318). Among these fishes the tripartite basi- and exoccipital facets are arranged in a variety of ways.

Rosen & Patterson (1969) recognised two general apomorphic conditions of the condyle in acanthomorph lineages. The paracanthopterygians they examined have the exoccipital facets displaced laterally, losing contact with the basioccipital facet, whereas, in the acanthopterygians they examined the exoccipital facets were displaced dorsally. Thus, the mastacembeloid arrangement in which the basi- and exoccipital facets are firmly joined into a single tripartite, concave socket is considered to represent an even more derived condition. However, this arrangement is not unique to mastacembeloids as the facets are also developed into a single concave socket in myctophids, polymixids and ammodytoids. In, for example, *Myctophum punctatum* (illustrated by Rosen & Patterson, 1969: fig. 61D) the anterior face of the first centrum is tightly fused with the occipital socket and cranial movement must be considerably restricted.

The tripartite occipital socket in *Polymixia japonica*, a species recently interpreted by Zehren (1979) as a basal percomorph, was also illustrated by Rosen & Patterson (1969: fig. 61E). In this taxon the anterior face of the first centrum has expanded into a convex condyle that fits into the occipital socket. This convexity of the first centrum may be the result of

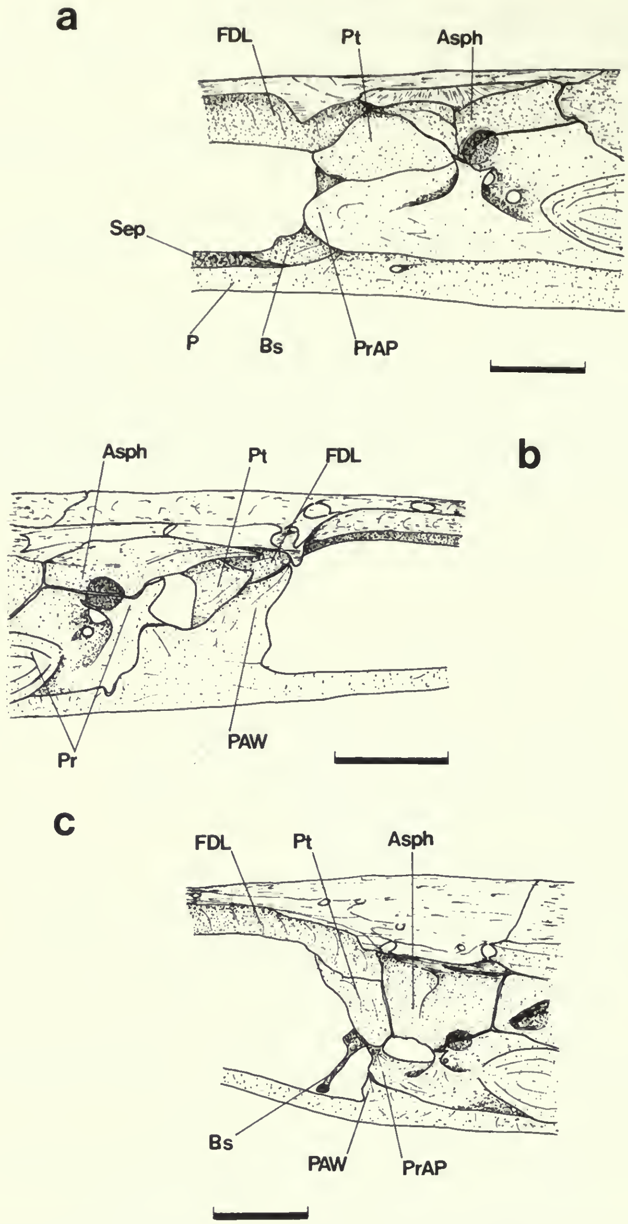

Fig. 4 Lateral view of neurocranial otic region in; (a) *Pholidichthys leucotaenia,* left side; (b) *Xiphistes mucosus,* right side; (c) *Ammodytes tobianus,* left side.

the osteoid cone (Patterson, 1975) having fused with it and the anterior part of the cone becomes rounded to fit into the occipital facet.

This apomorphic development of the anterior face of the first centrum has been taken a stage further in mastacembeloids. Here the anterior face is produced into a hemispherical condyle, that functionally forms a 'ball and socket' joint between the vertebral column and neurocranium. This is a synapomorphy of all mastacembeloids and is important evidence in support of the monophyletic origin of the group (see p. 108). In no other acanthopterygians, apart from the ammodytoids (Gosline, 1963), is there a 'ball and socket' joint between the vertebral column and neurocranium. Although the arrangement of the joint in ammodytoids is of a similarly derived type, in the absence of any further derived characters shared by these fishes it is thought that the resemblance is homoplastic.

The absence of a posttemporal bone was first noted by Regan (1912) in *Mastacembelus armatus* and is confirmed by all mastacembeloid taxa I have examined. In place of the posttemporal, 1–3 ossified tubules occur in most species.

Among teleosts, the only other groups lacking a posttemporal bone are the anguilloids, for example *Anguilla anguilla,* the notacanthids (McDowell, 1973: 137) and some siluroids (G. Howes, pers. comm.).

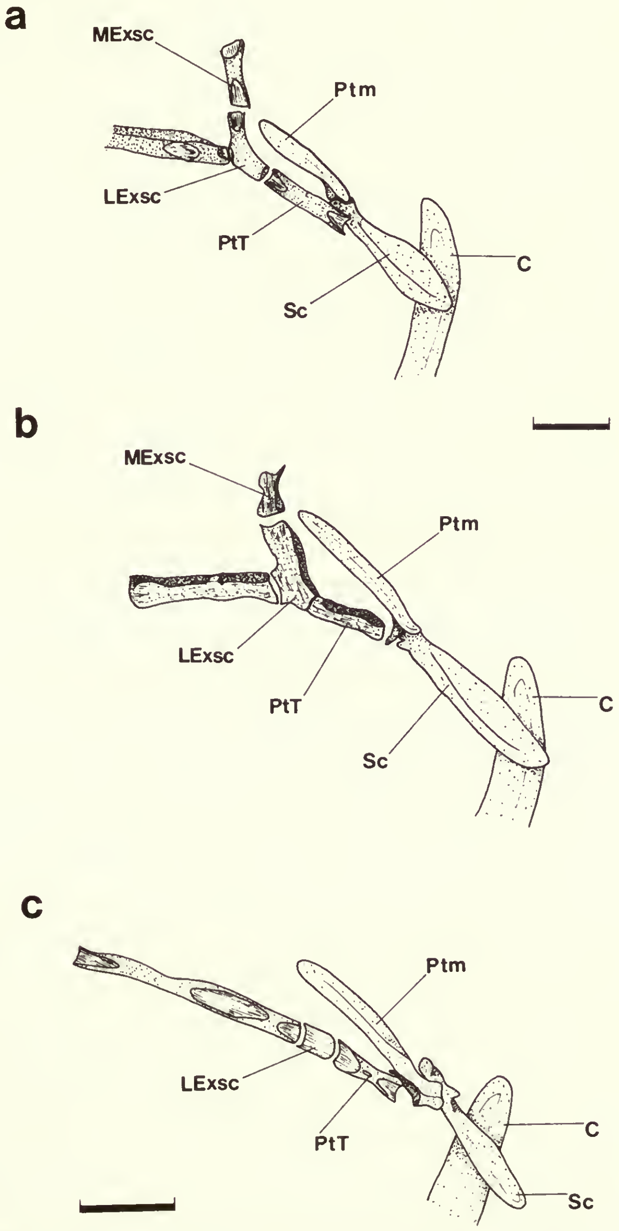

Fig. 5 Articulation of the left posttemporal bone to the pectoral girdle in: (a) *Zoarces viviparus;* (b) *Lycodes brevipes;* (c) *Dadyanos insignis.* Viewed obliquely from a dorsolateral position.

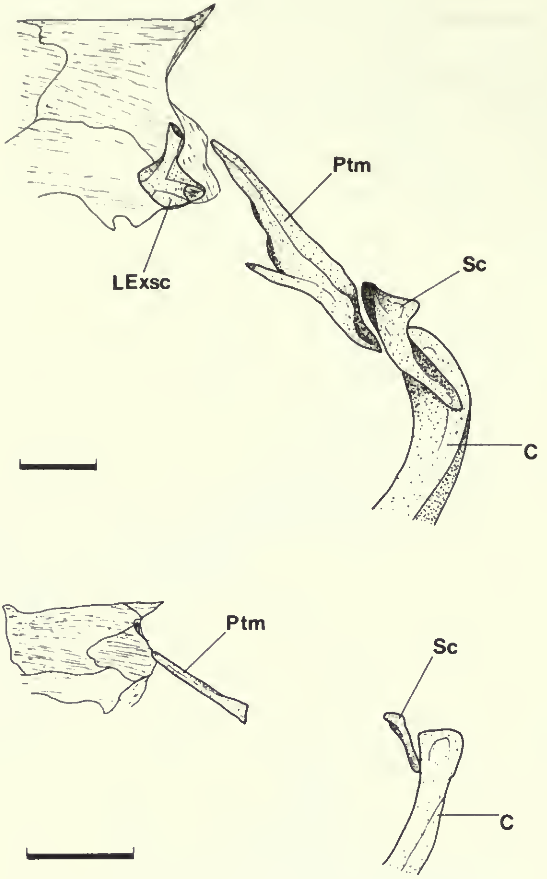

Fig. 6 Articulation of the left posttemporal bone in: (a) *Monopterus albus*; (b) *Synbranchus marmoratus.* Lateral view of the elements which are depicted *in situ.*

In the true eels the pectoral girdle lies posterior to the cranium, adjacent to the 7th or 8th abdominal vertebrae. The postcranial sensory canal in *Anguilla* passes through three small dermal tubules lying between the cranium and pectoral girdle.

Zoarcoids, for example *Zoarces viviparus, Lycodes brevipes* and *Dadyanos insignis* (Fig. 5), are also distinguished by their eel-like shape and posteriorly displaced pectoral girdle. This is connected to the neurocranium (epioccipital) by a narrow, blade-like posttemporal bone, through which the postcranial sensory canal does not run; instead it passess laterally, parallel to the posttemporal and is housed in two ossified dermal tubules.

From the condition in zoarcids it seems reasonable to conclude that the ossified postcranial tubules in mastacembeloids and some anguilloids are not necessarily remnants of the posttemporal.

The absence of a posttemporal distinguishes mastacembeloids from all other neoteleosts. Its loss, like that in some anguilloids (discussed above) and notacanthids (McDowell, 1973), is correlated with the posterior position of the pectoral girdle, (see Travers, 1984: 73).

The synbranchids also come into the category of eel-like neoteleostean fish with a reduced, posteriorly displaced pectoral girdle. A well-developed, forked, posttemporal connecting the basicranium to the pectoral girdle (generally adjacent to the 3rd & 4th abdominal vertebrae) occurs in *Monopterus albus* (Fig. 6a) and *Ophisternon* (Rosen & Greenwood, 1976: 63). On the other hand, in *Synbranchus* (e.g. *S. marmoratus*, Fig. 6b) the posttemporal is reduced to a narrow blade-like bone that tapers posteriorly from the basicranium (to which its anterior end is attached) and is not in contact with the pectoral girdle. The tendency in synbranchids towards reduction in size of the posttemporal is probably related to the position of the pectoral girdle. In its most derived condition (e.g. *S. marmoratus*) the posttemporal has lost its connection to the supracleithrum, an arrangment which, although unique to the synbranchids, could represent an early stage in the transformation of this bone to its condition in the mastacembeloids (i.e. complete loss). Unfortunately, suitable material of the most plesiomorph synbranchid—*Macrotrema elegans*—was not available for study.

Extrascapular bones are absent in all mastacembeloid taxa, (with the exception of *Mastacembelus brachyrhinus,* discussed below). The supratemporal arm of the cephalic sensory canal is completely enclosed in a transverse tube that passes across the parietal (Travers, 1984: 72). This canal surfaces at the medial edge of the parietal, and crosses the supraoccipital as an open channel, joining its partner in the midline.

The position of the supratemporal arm of the cephalic sensory canal in mastacembeloids may be the result of the lateral and medial extrascapulars (which generally house the canal) fusing along the posterodorsal surface of the parietal, or because true parietals have been replaced by extrascapulars (McDowell, 1973: 25). Alternatively, the extrascapulars may have been lost and the supratemporal sensory canal enclosed by the parietals during ontogeny.

In all mastacembeloids the parietal has a posterolateral flange (Travers, 1984: 72) that lies along the dorsal junction of the pterotic and epioccipital, and encloses the most lateral region of the supratemporal sensory canal. The expansion of the parietal in this region suggests that the extrascapulars may have fused with its posterodorsal surface, presumably in a manner similar to that described by Patterson (1977: 98) for the fusion between the median extrascapula and the supraoccipital in primitive clupeomorphs. Furthermore, in *Mastacembelus paucispinis* (Travers, 1984: fig 35a & c) a short, independent tubule, reminiscent of the posterior tubule-like region of the lateral extrascapula in other perciforms (e.g. *Perca fluviatilis*), is fused to the parietal between the pterotic and epioccipital. In my specimen of *Mastacembelus brachyrhinus* (uniquely among mastacembeloids) there is an independent lateral extrascapula on the dorsal surface of the parietal (albeit on the left side only, Travers, 1984: fig 37a & c).

The lateral and medial extrascapulae in higher euteleosts are short tubules which house the supratemporal arm of the cephalic sensory canal system as it traverses the dorsal surface of the neurocranium. Extrascapulae of this type are of widespread occurrence in the gadiform, batrachiodiform, cyprinodontiform, beryciform, scorpaeniform and perciform assemblages. In some of these the lateral and medial extrascapulae may be fused to the underlying parietal (dorsal surface), as seen for example, in the zoarcoids (e.g. *Zoarces viviparus* & *Lycodes muraena*) and some blennioids (e.g. *Malacoctenus delalandei, Haliophus guttatus, Acanthemblemaria maria* & *Congrogadus subduceus*). In all these examples the extrascapulae, although fused to the parietal, are clearly distinguishable, retaining their overall shape and size. However, in other blennioids including members of the Blenniidae (Springer, 1968) and Stichaeoidea (Makushok, 1958: his Stichaeoidae), extrascapulae are absent and the supratemporal sensory canal lies within the parietal. This arrangement of the supratemporal sensory canal, apart from the mastacembeloids, is found only in these blennioids among the teleosts examined.

In some percomorphs, however, the extrascapulae and the supratemporal arm of the sensory canal are both absent, for example in the gobioids and synbranchoids, as well as in *Chaudhuria* and *Pillaia* among the mastacembeloids (see below).

Thus, the total absence of discrete extrascapulae in mastacembeloids is a derived feature shared only with some blennioids. The lack of a supratemporal commissural sensory canal in *Chaudhuria* and *Pillaia,* taxa in which there appears to be a progressive reduction in the extent of the cephalic sensory canal system (see p. 113), may well be a further stage in such a trend (one convergent with that in the gobioids and synbranchoids).

JAWS

The upper jaw in mastacembeloids is non-protrusile and in this respect is rather exceptional among percomorphs; indeed, jaw protrusibility is a characteristic feature of most neoteleosts (Liem & Lauder, 1983).

Among percomorph fishes, relatively long premaxillary ascending processes and maxillary cranial condyles are absent only in the synbranchids and the mastacembeloids. The simple non-protrusile jaws in these taxa are similar to the plesiomorph teleostean condition seen in the osteoglossomorph, elopiform, clupeomorph and protacanthopterygian assemblages. Although the non-protrusile jaws in mastacembeloids and synbranchids appear to be of this type they have presumably been secondarily redeveloped from protrusile jaws (see Gosline, 1983: 324, discussed below p. 109 & 129).

The mastacembeloid dentary has a posteroventral extension (Travers, 1984: 80) which tapers posteriorly. This process extends from the rim of the posterior sensory canal opening and lies along the ventral edge of the anguloarticular. In representatives from nearly all major teleostean lineages (particularly neoteleosts) the posterior opening of the sensory canal in the dentary marks the posteroventral tip of this bone; e.g. in *Osteoglossum* (Kershaw, 1976); *Elops* (Forey, 1973); *Anguilla; Denticeps* (Greenwood, 1968); *Cyprinus; Salmo; Maurolicus; Chlorophthalmus; Myctophum; Percopsis; Gadus; Ophidion; Holocentrus* and *Serranus.*

In the numerous lower jaws taken from a wide selection of basal teleosts and illustrated by Nelson (1973), only that in *Arapaima gigas* (Nelson, 1973: fig. 2c & d) shows a process comparable with that in mastacembeloids, and must be considered a homoplasy. The dentary of *Arapaima gigas* illustrated in lateral view by Kershaw (1976: fig. 20, redrawn after Ridewood 1905) shows no posteroventral extension beyond the posterior opening of the sensory canal (the latter being clearly indicated); however, I have examined a skeletal preparation of *Arapaima gigas* and the long posteroventral process is clearly present.

Of the remaining lower jaws illustrated by Nelson there is a posteroventral extension of the dentary beyond the posterior sensory canal pore (albeit to a lesser extent than in the mastacembeloids) in some engraulids e.g. *Coilia mystus* and *Thrissina baelama* (Nelson, 1973: fig. 5 C, D & E, F).

Both these taxa are characterised by a long, pointed mandible, and the short posterior projection on the dentary may be regarded as homoplastic with that in mastacembeloids and *Arapaima.*

Among euteleosts, the synbranchids are the only group (apart from the mastacembeloids) in which there is a long posteroventral process on the dentary (illustrated by Rosen & Greenwood, 1976: fig. 60 & 61). This process extends beyond the posterior sensory canal opening along almost the entire ventral edge of the anguloarticular. Thus, it seems reasonable to conclude that the posterior extension of the dentary is a synapomorphy uniquely shared by mastacembeloids and synbranchids among euteleostean fishes.

The mastacembeloid mandible is also exceptional in the size and position of its coronomeckelian, a large bone (relative to the other mandibular elements) lying across the anterolateral face of the suspensorium.

A small coronomeckelian on the medial face of the anguloarticular is of common occurrence throughout the teleostomes (Starks, 1916), and this is taken to represent the plesiomorph condition both with regard to its size and position.

The coronomeckelian was shown by Starks (1916) to be the ossified anterior end of the A_3 tendon. In support of this view he cited the condition of these elements in *Spheroides annulatus* '... where the adductor tendon has obviously ossified for a short space leaving an interval of tendon between the ossified portion and the mandible'.

This interpretation can also be applied to the arrangement of the coronomeckelian in mastacembeloids, except that in these fishes the tendon has ossified dorsal to the mandible. Tendons may become ossified (forming a sesamoid bone) in regions where tendon movement produces opposing frictional forces, for example where the tendon runs across a bony prominence. The long A_3 tendon in mastacembeloids runs across such a prominence—the deep and somewhat bulbous anterolateral face of the ectopterygoid (Travers, 1984: fig. 5).

The development of the unusually large, dorsally situated coronomeckelian in mastacembeloids thus appears to be directly related to the shape of the ectopterygoid. The size and position of the coronomeckelian in *Chaudhuria* and *Pillaia* (discussed below), taxa which lack an ectopterygoid with a deep anterolateral face, is evidence in support of this view.

Although there is extensive variation in the size and shape of the coronomeckelian among teleosts, (see Fig. 7 a–g) in no other taxon is it comparable with that in mastacembeloids, for which it is taken to be a unique synapomorphy.

The dorsal edge of the anguloarticular is straight in most mastacembeloids (Travers, 1984: 82) and lacks a coronoid process in all taxa except *Macrognathus,* where the coronoid elevation is low and broad based (see Travers, 1984: 80).

The anguloarticular lacks a coronoid process in about half the synbranchid species recognised by Rosen & Greenwood (1976: 45), and this characteristic was considered to be of some phylogenetic interest by these authors. They were of the opinion that, 'Such coronoid prominences on the articular of teleosts are common, although in many unrelated fishes with elongate crania and jaws the process is absent'. The absence of a coronoid process on the anguloarticular in synbranchoids was thought by Rosen & Greenwood (1976) to be a plesiomorph feature of the taxon, and the processes present in *Monopterus albus* and *Ophisternon* species were thought to be independently gained autapomorphies.

A coronoid process is absent on the anguloarticular in a variety of teleosts including the anguilloids (e.g. *Anguilla anguilla*), some percoids (e.g. *Scarus croicensis*), blennioids (e.g. *Notograptus guttatus* and *Pholidichthys leucotaenia* [very low projection]), many gobioids (e.g. *Gobius niger; Aphia minuta; Amblyopus brousonetti* and *Crystallogobius linearis*), and notothenioids (e.g. *Notothenia sema* [very low projection]). These observations support the view held by Rosen & Greenwood (op. cit.) that many unrelated fishes lack a coronoid process and that its absence in percomorph lineages is plesiomorphic.

PTERYGO–PALATINE ARCH

Regan (1912) found that in mastacembeloids the '... pterygoid is movably articulated with the lateral ethmoids external to the palatine', and noted that they are 'very perculiar' in these fishes.

The ectopterygoids are large bones characterised by a deep anterolateral face and their direct connection to the lateral ethmoids (Travers, 1984: 83). This direct articulation of the large ectopterygoid (functionally replacing the palatine which lacks articulatory facets; see below) is the sole means by which the anterior end of the suspensorium is joined to the neurocranium in most mastacembeloid taxa. The articulation of the suspensorium to the neurocranium in almost all other euteleosts involves the palatine. Among lower teleosts, the palatine also plays a central role in suspensorial articulation with the neurocranium, although this does not necessarily exclude the ectopterygoid from having an articulatory function in some taxa, as for example in the osteoglossoids. In *Osteoglossum* there is only a single element in place of the ectopterygoid and palatine, which are, in the opinion of Kershaw (1976: 192), 'indistinguishably connected'. The anterior end of the 'ecto-palatine' bone is ligamentously connected to the lateral ethmoid in *Osteoglossum.*

The ectopterygoid is enlarged anteriorly in some halosauroids (Greenwood, 1977); however, in none does it articulate directly with the ethmoid region. Anguilloids too generally have an elongated suspensorium and in *Anguilla anguilla* (Fig. 8) its anterior articulation is effected by a long, narrow bone which extends to the ethmoid region and may incorporate the palatine (the palatopterygoid of Matsui & Takai, 1959) because an ossified autopalatine was not observed in *Anguilla.* This bone was considered by Norman (1926) to be an endopterygoid.

More recently, Leiby (1979 & 1981) has found that in several ophichthid anguilloids the endopterygoid and metapterygoid form a single compound bone which fuses during ontogeny with the anterior edge of the hyomandibula. He identifies the long narrow bone connecting the suspensorium and neurocranium as an ectopterygoid in these fishes (Leiby, 1979: fig. 2F & 1981: fig. 12A).

The suspensorium in *Anguilla* has, superficially, a remarkably similar apearance to that in several of the more highly derived mastacembeloids, particularly *Chaudhuria* and *Pillaia*

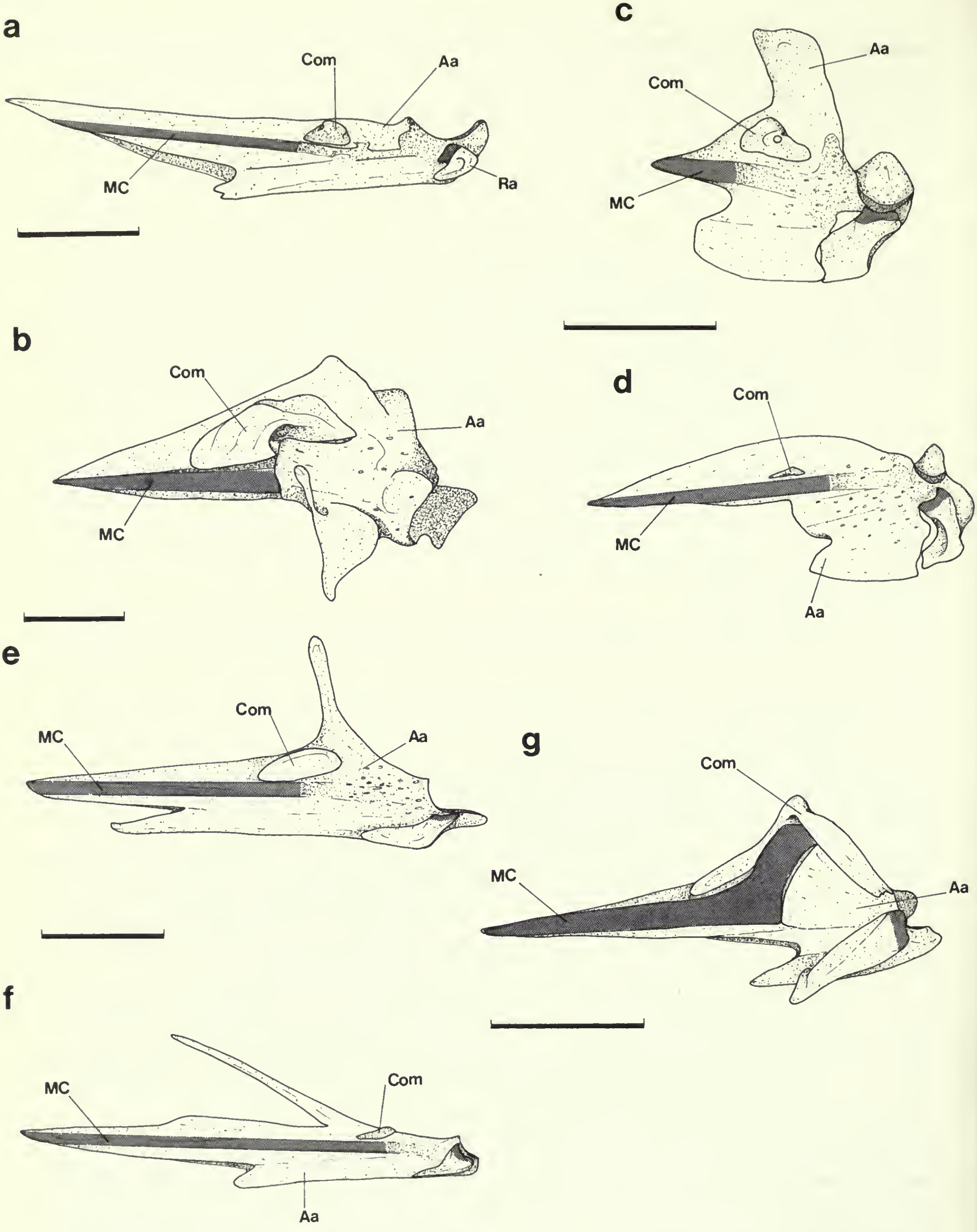

Fig. 7 Medial view of the right coronomeckelian in: (a) *Notograptus guttatus*; (b) *Rhyacichthys aspro*; (c) *Trichogaster leeri*; (d) *Sandelia capensis*; (e) *Luciocephalus pulcher*; (f) *Hypoptychus dybowskii*; (g) *Callionymus lyra.*

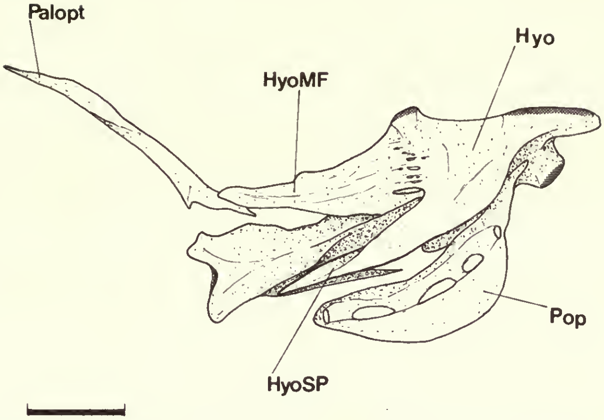

Fig. 8 *Anguilla anguilla,* left hyopterygoid arch and preoperculum in lateral view.

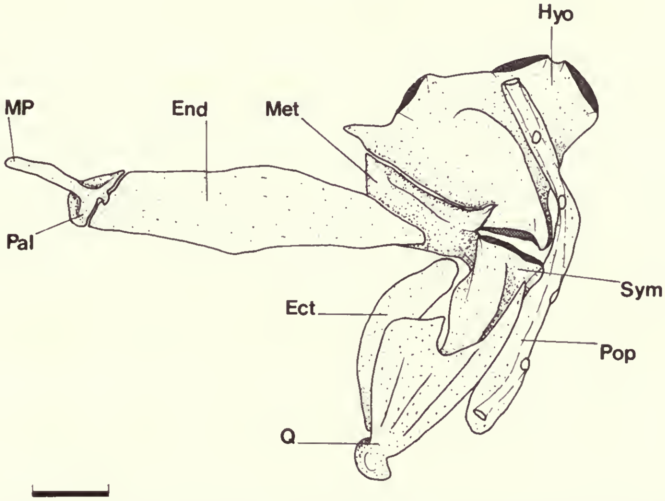

Fig. 9 *Congrogadus subduceus,* left hyopalatine arch and preoperculum in lateral view.

(e.g. compare Travers, 1984: figs. 17 & 25 with Fig. 8). However, its anterior articulation in *Anguilla* is effected by what is apparently the ectopterygoid (which may have fused with the palatine) articulating with the ethmoid region and maxilla, whereas, in *Chaudhuria* and *Pillaia* the ectopterygoid, which is also attenuated (and possibly fused with the palatine), articulates with the lateral face of the vomerine shaft (see Travers, 1984: 83).

The endopterygoid is enlarged, functionally replacing the ectopterygoid, in the congrogadids. In *Congrogadus subduceus* and *Haliophus guttatus* (Fig. 9) the anterior end of the bone is connected to the palatine which articulates the suspensorium with the neurocranium. The ectopterygoid in these species is a short, narrow bone connected to the anterior edge of the quadrate, and lacks an anterior point of articulation with the skull.

In synbranchids there is a large ectopterygoid which Rosen & Greenwood (1976: 44–48) imply is associated with the absence of the endopterygoid and with the massive development of the basisphenoid. They term this trend one of the 'special' attributes of all synbranchids. In *Synbranchus marmoratus* (Fig. 10) the ectopterygoid is connected posteriorly (by its anterodorsal, but subdistal process) to a basisphenoid projection, and also has a more usual distal articulation with the palatine. This additional abutment has developed between the ectopterygoid and frontal in *Ophisternon aenigmaticum* (Gosline, 1983: fig. 3B). The degree

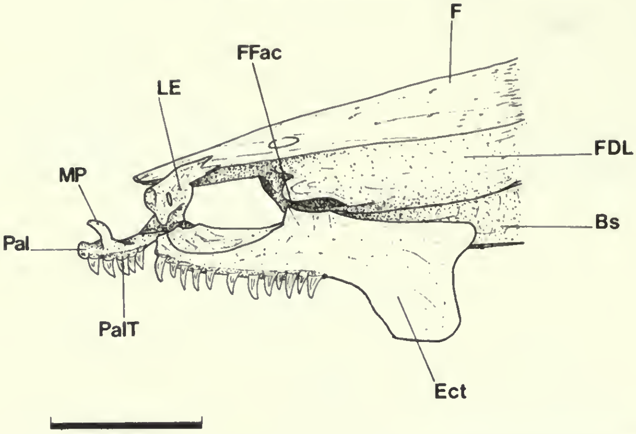

Fig 10 *Synbranchus marmoratus*, left palatopterygoid articulation to the neurocranium, lateral aspect.

of enlargement of the ectopterygoid is particularly great in *Monopterus albus* (compare Rosen & Greenwood, 1976: figs. 59 & 61).

The palatine in *Monopterus* lies further anteriorly than that in *Synbranchus* (e.g. compare Rosen & Greenwood, 1976: figs. 58 & 59) and its articulatory function (between suspensorium and lateral ethmoid) is taken over by the ectopterygoid in both species.

The increase in the size of the ectopterygoid in synbranchids (p. 110) must be an apomorphic feature because it culminates in the anterior displacement of the palatine (associated with a reduction in the size of its maxillary process and its close adherence to the vomerine shaft) and, consequently, the establishment of a direct articulation between the ectopterygoid and lateral ethmoid in some taxa (e.g. *Monopterus*).

Apart from these highly modified synbranchids, a direct articulation between the ectopterygoid and the lateral ethmoid is an otherwise distinctive synapormorphy found only in the majority of mastacembeloids.

A long, thin palatine sutured along the posterolateral face of the vomerine shaft, and lacking articulatory facets, is a characteristic feature of most mastacembeloid taxa.

In those euteleosts with a distinct palatine this bone generally has moveable joints with the neurocranium and the upper jaw, *viz.,* with the lateral ethmoid, usually involving a medial palatine facet, and anteriorly with the maxilla (cranial condyle) usually involving a short, often curved, maxillary process developed from the palatine. Although the palatine in higher euteleosts is variable in shape and dentition it was found to possess these articulatory functions in most lineages except the mastacembeloids and synbranchids.

The mastacembeloid palatine is a straight bone that is sutured to the lateral face of the vomer/parasphenoid junction below the lateral ethmoid to which it may be connected by a weak ascending spur (Travers, 1984: 84). It lacks any moveable articulation and does not have a maxillary process. Posteriorly, the palatine extends below the orbit, is dorsoventrally flattened, and supports the anterior fibres of the *adductor arcus palatini* muscle in this region. This highly derived palatine is typical of all mastacembeloids and is presumably associated with the lack of a protrusile upper jaw.

The reductional trend in the synbranchid palatine is probably also associated with the loss of protrusibility of the upper jaw.

In the more highly derived synbranchids (e.g. *Monopterus*) both the close adherence of the palatine to the vomerine shaft, and the lack of its connection to the lateral ethmoid are derived features (synapomorphies) shared with the mastacembeloids but with no other higher euteleosteans. Development of the mastacembeloid palatine appears to be at a more derived stage (i.e. no maxillary process or connection to the ectopterygoid) than is the synbranchid palatine. This arrangement of the palatine in mastacembeloids and synbranchids is closely associated with the development of the ectopterygoid in these taxa and, in combination, these characters provide important evidence in support of an hypothesis of shared common ancestry for the two groups, evidence consistent with the indications provided by the dentary (see p. 98) and posttemporal (p. 96) bones.

BRANCHIAL ARCHES

In most mastacembeloids a small, round, toothplate is fused to the dorsal surface of hypobranchial 3 (see also Maheshwari, 1965: fig. 6). Apart from these fishes a fused toothplate features (see p. 103), it could be a reliable synapomorphy for uniting these groups. Its (e.g. *Nandus* & *Badus*) and channids (e.g. *Channa*). The possible means by which this fused toothplate has developed in *Nandus, Badus* and *Channa,* and its value as an indicator of phyletic relationships were discussed by Nelson (1969: 496–7).

A fused toothplate on hypobranchial 3 is absent in *Mastacembelus mastacembelus, Pillaia* and in an assemblage of African species (Travers, 1984: 94).

In those species in which the toothplate is present, it is not always opposed by toothplates on epibranchial 1. Toothplates on that element occur only in the larger predaceous species (e.g. *Mastacembelus cunningtoni;* Travers, 1984: fig. 64). Although a fused toothplate on hypobranchial 3 is a synapomorphy uniting most mastacembeloids, its mosaic distribution within the group and its occurrence in several phylogenetically distantly related taxa make it a character of limited taxonomic value when considered in isolation.

A pair of processes descending from the posterolateral corners of basibranchial 2 are present in most mastacembeloids. The ventral tips of these processes are curved anteriorly and connect by converging ligaments to the posteroventral margin of basibranchial 1 (Travers, 1984: 92). Processes on basibranchial 2 have not been found in any outgroup taxa, their presence is treated as a synapomorphic character of the mastacembeloids, and further evidence in support of their monophyletic origin.

DORSAL FIN SPINES

The development of a series of spinous rays in the dorsal fin is a feature common to most acanthopterygian fishes. The number of dorsal spines may vary from a short row to a long series along the entire length of the dorsal surface in some fishes, e.g. the 'prickleback', *Stichaeus hexagrammus.* The spinous dorsal rays, regardless of their number, are generally interconnected by a thin membrane, however, this is absent in mastacembeloids.

Isolated dorsal spines appear also in several notacanthid halosauroids. However, the spinous rays in these fishes have been shown by McDowell (1973: 143) to form '... part of a (single dorsal) connected fin ... that is low and so heavily sheathed by scaly skin that only the separate tips of the spines are visible without dissection'. Furthermore, all these fishes lack a series of soft-rays posterior to the spinous part of the dorsal fin.

Thus a dorsal fin composed of isolated short, stout spines anterior to a long series of soft rays must be a synapomorphy of the mastacembeloids as it is unique to the group.

Myology

CEPHALIC MUSCLES

A number of myological features common to several mastacembeloid taxa were found to be unique to the group.

The mastacembeloid *levator operculi* originates from the pterotic and inserts on the dorsolateral face of the operculum in all taxa examined (Travers, 1984: 119). The insertion of a *levator operculi* was described by Winterbottom (1974: 238) as the dorsal or dorsomedial face of the operculum. This is the condition in the majority of teleosts I have examined, and must be considered the plesiomorphic condition in neoteleosteans. A lateral insertion of fibres of the *levator operculi,* apart from in the mastacembeloids, was only found in species of the phylogenetically distantly related anguilloids (e.g. *Anguilla anguilla*), synbranchoids

(Liem, 1980*a*: 83) and blennioids (e.g. *Notograptus guttatus*). The lateral insertion of *levator* fibres in all mastacembeloid and synbranchoid taxa suggests that, together with several other features (see p. 103), it could be a reliable synapomorphy for uniting these groups. Its occurrence in anguilloids and some blennioids in the absence of any further derived characters shared by these taxa and the mastacembeloids and synbranchoids, is interpreted as a convergence.

A small independent muscle lies between the posterior edge of the preoperculum and anterolateral face of the operculum (ventral to the opercular lateral ridge) in all mastacembeloids (Travers, 1984: fig. 79a), and is termed the '*musculus intraoperculi*' (Travers, 1984: 120) because of its position within the opercular series. Winterbottom (1974) describes no

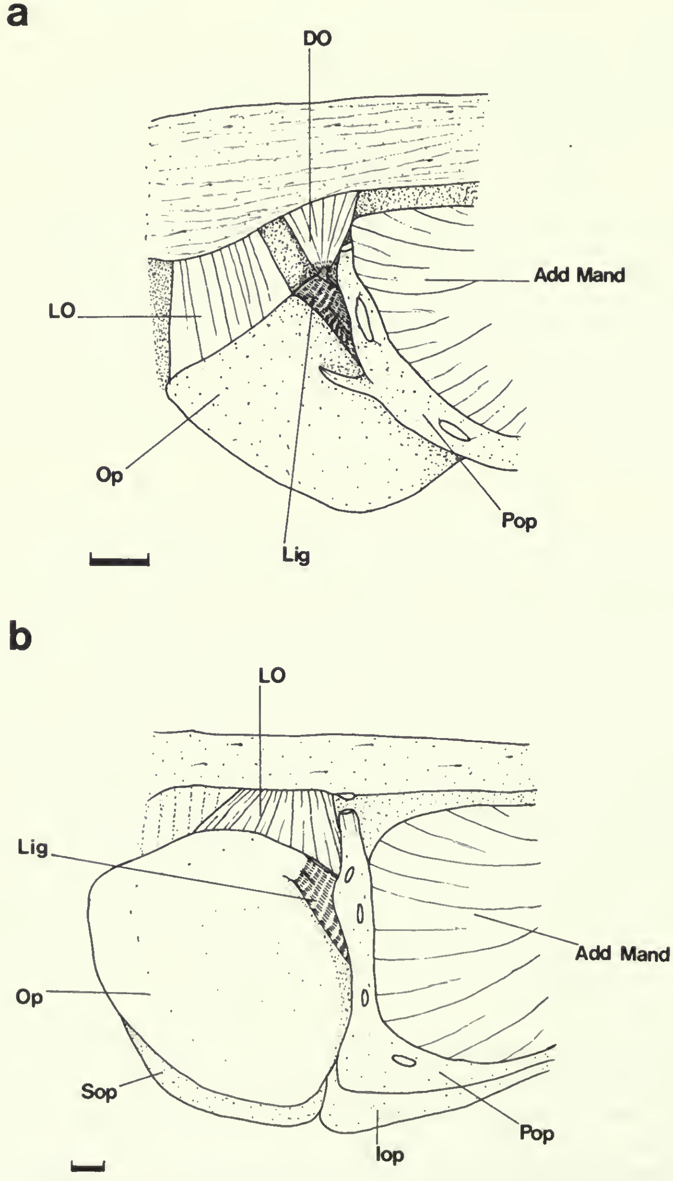

Fig. 11 Ligamentous connection between the preoperculum and operculum in: (a) *Cottus gobio*; (b) *Channa obscura*. Lateral view, right side.

muscle in this position in any teleost he examined; its absence is confirmed by all outgroup taxa I have examined. Its unique occurrence in the mastacembeloids is a valuable synapomorphy for the group.

A ligament between the posterior edge of the preoperculum and the anterolateral face of the operculum occurs in a number of phylogenetically diverse acanthomorph taxa. These include the cottoids (e.g. *Agonus cataphractus*, with a weak ligament between the preoperculum and operculum and *Cottus gobio* with a broad strong ligament; Fig. 11a), the gobioid *Amblyopus broussonetti* (in which a broad, weak collagenous band lies between the preoperculum and operculum) and the channoids (e.g. *Channa obscura*, with a strong opaque ligament; Fig. 11b).

An origin of the *adductor hyomandibulae* from the posteroventral surface of the parasphenoid is not recorded by Winterbottom (1974: 240), but this condition is typical of all mastacembeloids (Travers, 1984: 125). Also, a musculous insertion of this muscle partly on the medial face of the symplectic seems to be a general feature of all mastacembeloids and one not found in other groups (Winterbottom, 1974 gives the muscle's insertion site as the 'posterodorsomedial face of the hyomandibular').

The arrangement of these features of the *adductor hyomandibulae* were not always readily discernible in the outgroup taxa I examined they, therefore, remain doubtful additional synapomorphies of the group.

The dorsal expansion of fibres of the *hyohyoidei adductores* above the upper branchiostegal rays (medial to the suboperculum and operculum) and their insertion on the cleithrum, supracleithrum and posttemporal tubules in mastacembeloids (Travers, 1984: 128) is an unparalleled apomorphic development of this muscle. The general condition of the *hyohyoidei adductores* in teleosts is as a medial sheet of fibres extending only between the distal portions of the branchiostegal rays. Winterbottom (1974) noted that the fibres may continue dorsally above the posterodorsal ray to attach to the medial faces of some of the opercular bones, but in no teleost did he find the dorsal expansion continuing above the operculum and across the lateral face of the body muscles. I have examined the *hyohyoidei* in representatives of each major teleostean lineage, particularly those in which the opercular opening is restricted.

The anguilloids, e.g. *Anguilla anguilla,* have a very restricted opercular opening effected in part by the filiform branchiostegal rays which curve up around the posterodorsal corner of the operculum; see McAllister (1968: 79). Fibres of the *hyohyoidei adductores* pass across the medial face of these long branchiostegal rays, but do not extend further dorsally or insert on the lateral face of the body. McAllister (*op. cit.*) found a close resemblance between the anguilloid branchiostegal arrangement and that in the myctophoids. Here the *hyohyoidei adductores* are of general teleostean proportions.

The ophidioids (e.g. *Carapus acus*), zoarcoids (e.g. *Zoarces viviparas*) some blennioids (e.g. *Pholis gunnellus*), callionymoids (e.g. *Callionymus lyra*) and the tetraodontoids (e.g. *Diodon*) are all acanthomorph lineages with some restriction of the opercular opening. In none, however, do the *hyohyoidei* expand across the lateral wall of the body, although in some tetraodontoids they may expand medially and contact their partners in the midline (Winterbottom, 1974).

The synbranchids (particularly members of the Synbranchinae; Rosen & Greenwood, 1976) have a very restricted opercular opening. The 4–6 branchiostegal rays may have their distal halves poorly ossified in a number of synbranchids (Rosen & Greenwood, 1976), and although the family is characterised by small opercular bones, the branchiostegal apparatus and its musculature are hypertrophied (Liem, 1980*a* & *b*; fig. 14 in each). The fibres of the *hyohyoidei adductores* lie laterally across the branchiostegal rays in *Synbranchus marmoratus* (Fig. 12) and expand dorsally (the fibres running vertically, medial to the operculum) to a point above the operculum and over the lateral wall of the body (see also Liem, *op cit.*). The anterior fibres of the *hyohyoidei* in these synbranchids are also expanded dorsally (medial to the preoperculum), and form a distinct muscle slip, whose dorsolateral fibres insert on the medial face of the preoperculum and the anteromedial face of the

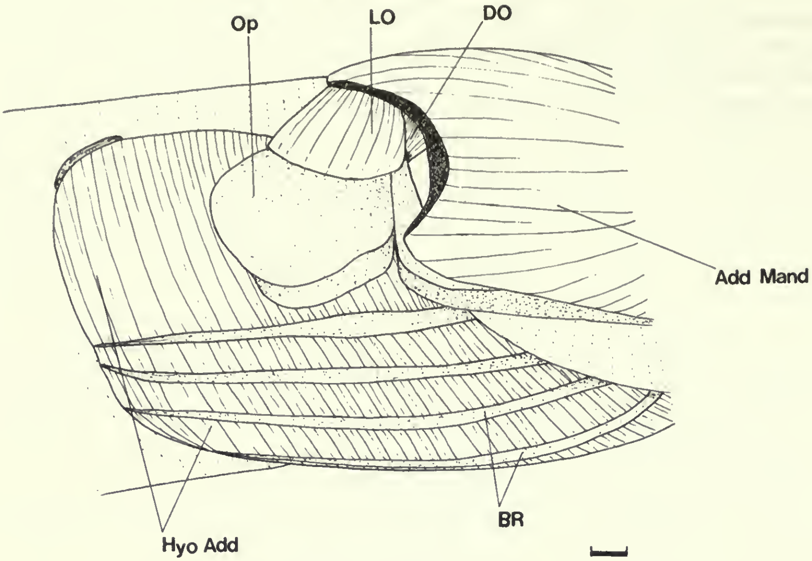

Fig. 12 *Synbranchus marmoratus,* right *hyohyoidei adductores* muscle, in lateral view after removal of the skin and part of the superficial *adductor mandibulae* musculature (to expose the *levator* and *dilatator operculi* muscles).

operculum, crossing the lateral border between these bones. Liem, however, makes no reference to this distinct anterodorsal slip of muscle fibres in either *Synbranchus* or *Monopterus.* Unfortunately, material of *Macrotrema caligans,* the most plesiomorphic synbranchid (Rosen & Greenwood, 1976) which has a comparatively unrestricted operculum (relative to other synbranchids), was unavailable for dissection.

The *hyohyoidei adductores* were considered by Liem (1980*a* & *b*; his *hyohyoideus*) as probably '. . . the most specialized muscle in synbranchiforms' as it is large and thick, occupies the entire ventrolateral surface of the branchial region and has its dorsal region (*hyohyoideus superior*) developed to such an extent that the upper fibres pass between the 1st and 2nd branchiostegals to the operculum (inner aspect) and pectoral girdle (supracleithrum & cleithrum). This arrangement of the *hyohyoidei adductores* closely resembles that in mastacembeloids (see Travers, 1984: fig. 79a and compare with fig. 14 in Liem, 1980*a* & *b*) and is an important synapomorphy of these taxa and further evidence in support of their hypothesised sister group relationship (see p. 104). This evidence is corroborated by the anterior slip of muscle fibres on the *hyohyoidei* in synbranchids, since a lateral migration of these fibres between the posterior edge of the preoperculum and anterolateral face of the operculum would result in a muscle having the same position and skeletal relationships as the '*intraoperculi*' muscle of mastacembeloids.

The presence of this muscle slip in synbranchids suggests that the mastacembeloid '*intraoperculi*' muscle could have developed from the *hyohyoidei adductores.* The innervation of the '*intraoperculi*' may well give a useful clue to its origin. If developed from the *hyohyoidei* the mastacembeloid arrangement should be considered as phylogenetically more advanced than that of the synbranchids.

The anterior tendinous insertion of the *obliquus superioris* on the posteroventral edge of the exoccipital is a feature of all mastacembeloids (Travers, 1984: 128). Anteriorly, its fibres do not fuse with the ventral surface of the epaxialis musculature. The anterior insertion of the obliquus tendon is described by Winterbottom (1974: 296) as being on to the posterolateral otic region of the skull, often extending forward beneath the orbit along the parasphenoid and even reaching the vomer. An exoccipital insertion for the *obliquus superioris*

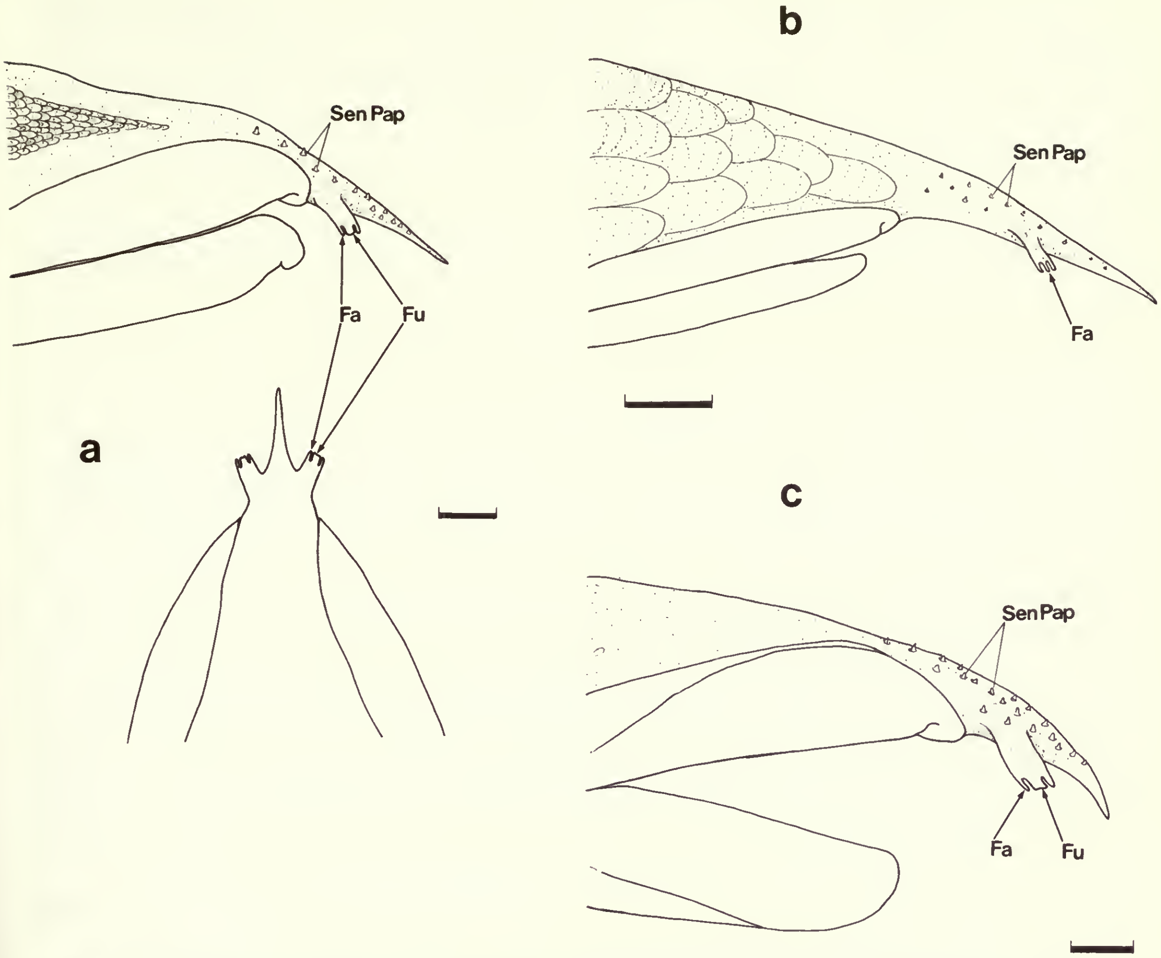

Fig. 13 Lateral view of the rostral appendage including the fimbriae and fimbrules surrounding the rim of the anterior nostril in: (a) *Mastacembelus moorii* (and dorsal view); (b) *Mastacembelus pancalus*; (c) *Mastacembelus mastacembelus*.

was not found in any other taxon than the mastacembeloids, and can be considered as a synapomorphy for the group.

The condition of Baudelot's ligament in mastacembeloids (Travers, 1984: 122 & 128) is uncharacteristic of its arrangement in higher enteleosts as described by Winterbottom (1974), who made no reference to it ever becoming bifurcated. Although dissection was not always possible, in those outgroups in which Baudelot's ligament was revealed on no occasion was it found to have a forked posterior end. The position of this ligament in mastacembeloids, with its dual connection to the pectoral girdle, appears to be a unique feature that may be tentatively interpreted as derived in comparison to the general arrangement and synapomorphous for the group.

Two other mastacembeloid features not found in any outgroup also warrant description: A rostral appendage, composed of two long, tubular extensions from the olfactory sacs lying on either side of a central rostral tentacle, is found in all but one mastacembeloid. This structure (described by Sufi, 1956 and Gosline, 1968: 61 & 1983: 323) is developed to a varying extent, from the very short appendage in *Mastacembelus moorii* (Fig. 13) to the large trunk-like appendage in *Macrognathus aculeatus* (Travers, 1984: fig. 45c & 46c).

A tubular anterior nostril is found in a number of phyletically diverse teleosts, from the anguilloids (e.g. *Anguilla anguilla*) to the channoids (e.g. *Channa obscura*). However, in none apart from the mastacembeloids, is the anterior tubular extension of the olfactory sac associated with a central rostral tentacle. Such a rostral appendage is an important synapomorphic character of the mastacembeloids, and is present in all taxa except *Chaudhuria*. The absence of a rostral appendage in this highly reduced and rather aberrant mastacembeloid is discussed below.

The presence, as in mastacembeloids, of a massive *nervus olfactorius* running through the centre of the lateral ethmoid (see Poll, 1973: plates IV & V), has not been found in any other teleostean lineage. This arrangement of the *nervous olfactorius,* particularly its massive size, is considered as synapomorphous for the mastacembeloids.

II. Defining characters of the Mastacembeloidei

The foregoing comparison of mastacembeloid anatomical characters with those in other teleostean fishes revealed 18 synapomorphies (represented by the 1st node in the cladogram Fig. 19) that may be used to support an hypothesis for the monophyletic origin of the Mastacembeloidei. In summary, these characters are:

1. Concomitant elongation of the supraethmoid, vomer and 1st infraorbital bone, accompanied by a long nasal with a broad dorsal surface.
2. Tubular lateral ethmoids.
3. Wide anterolateral face of the pterosphenoid and its ventro-medial connection to its opposite number; a feature associated with a very compressed basisphenoid.
4. Preorbital spine formed by the enlarged 1st infraorbital bone.
5. Long anterior process on the prootic that passes across the anterolateral (precommissural) wall of the braincase and into the orbital cavity.
6. Wide anterolateral flange on the sphenotic associated with the posterior position of the postorbital process.
7. Small saccular bulla housed entirely within the prootic.
8. Large coronomeckelian, lying dorsally across the anterolateral face of the suspensorium.
9. Ventral processes on basibranchial 2.
10. Long dorsal (and anal) fin composed of isolated short, stout spines unconnected by membrane, anterior to a long series of soft branched rays.
11. The presence of a '*musculus intraoperculi*'.
12. Anterior, tendinous insertion of the *obliquus superioris* muscle on the posteroventral edge of the exoccipital.
13. Baudelot's ligament forked posteriorly, connected to the supracleithrum and cleithrum, lying between the *obliquus superioris* and expaxialis muscles.
14. Anterior nasal openings at the end of long tubular epidermal extensions of the olfactory sac lying on either side of a central rostral tentacle.
15. Massive *nervus olfactorius* connecting the telencephalon with the olfactory organ.
16. Loss of lateral and medial extrascapular bones, associated with the incorporation of the supratemporal branch of the cephalic sensory canal system into the parietal.
17. Round toothplate fused to the dorsal surface of hypobranchial 3.
18. Development of the tripartite occipital facet into a concave socket, the anterior face of the first centrum into a hemispherical condyle and their articulation as a 'ball and socket' joint.

Of these synapomorphies, 1 to 15 do not appear in any other teleostean lineage examined as part of this study. These 15 features are unique to the mastacembeloids and conclusive evidence in support of the group's monophyletic origin. Of the remaining characters, 17 is shared mosaically, with a few and distantly related taxa; 16 is shared with some blennioids, and 18 is shared with the ammodytoids. Characters 16 to 18 are considered to be convergent in these taxa which do not share any other apomorphic features with the mastacembeloids.

On the basis of these synapomorphies the species at present recognised as constituting the mastacembeloids, i.e. *Chaudhuria caudata, Pillaia indica* (and *Garo khajuriai*: a second pillaiid species given separate generic status on the basis of slight superficial and morphometric dissimilarities, in a paper that became available only after this work had gone to press; Yazdani & Talwar, 1981), *Macrognathus siamensis, Macrognathus aral, Macrognathus aculeatus*, 15 Oriental *Mastacembalus* species (after Sufi, 1956) and about 46 African *Mastacembelus* species (see Travers, 1984: table I) are all placed in a single taxon whose categorical rank is discussed below.

III. Interrelationships of the Mastacembeloidei

In the past a variety of groups have been suggested as close relatives of the mastacembeloids (see Travers, 1984: table II). Although generally recognised as a member of the large and diverse order Perciformes (Regan, 1912 and Greenwood *et al.*, 1966), their interrelationships have remained obscure.

One mastacembeloid synapomorphy (18) occurs in a similar condition in the ammodytoids (excluding *Hypoptychus*, see p. 94). A close phyletic relationship between the mastacembeloids and this group has never been demonstrated and no other congruent apomorphies were found to substantiate a possible close relationship between these taxa. Another mastacembeloid synapomorphy (16) is found in a similar condition among the blennioids (see p. 97). A close phyletic relationship between the mastacembeloids and blennioids was originally proposed by Günther (1861), and has since received support from various authors (see Travers, 1984: table II). However, no further characters were found to substantiate such a relationship. On the contrary this proposal and that relating the ammodytoids to the mastacembeloids are falsified by 6 synapomorphies (19 to 24, and possibly 11 as well) shared with the synbranchoids, and thus indicate a more recent common ancestry for the synbranchoids and mastacembeloids. These 6 synapomorphies are:

19. Loss or reduction in size of the posttemporal bone, accompanied by loss of connection to pectoral girdle.
20. Extension of the dentary posteroventrally along the ventral edge of the anguloarticular.
21. Wide anterolateral face of the ectopterygoid and its direct articulation with the lateral ethmoid.
22. Palatine sutured along the posterolateral face of the vomerine shaft.
23. Insertion of the *levator operculi* muscle on the dorsolateral face of the operculum.
24. Dorsolateral expansion of the *hyohyoidei adductores* muscle, sealing the operculum to the body wall and causing a restricted opercular opening.

Two of these characters are shared uniquely by all mastacembeloid and synbranchoid (20 see p. 98 & 24 see p. 105) species examined. One character (23 see p. 103), apart from occurring in these groups, is also found in two other phylogenetically distantly related taxa. The three remaining characters (i.e. 19 see p. 96; 21 see p. 99 & 22 see p. 102) are not found in all synbranchoids. In those in which they do occur the characters are not generally at such an advanced stage of development as in the mastacembeloids. This may explain the synbranchoid condition of character 11, (the '*musculus intraoperculi*', see p. 104 above).

The phylogeny and systematics of the synbranchoids have been investigated by Rosen & Greenwood (1976). Although these authors found new evidence in support of the placement of these fishes in the Percomorpha, they were unable to offer any evidence of their interrelationships within the group and so retained them in a distinct order, Synbranchiformes. On the basis of the characters discussed above (19–24) I propose that the mastacembeloids, as the sister taxon of the synbranchoids, should be allocated to this order. Independent of my research, Gosline (1983) has recently published evidence that lends support to this proposal. The dissimilarity in the condition of the synapomorphies relating mastacembeloids and synbranchoids (apart from 20 & 24) may indicate an early dichotomy in the genealogical history of the group. Without evidence from fossil remains not even a minimum age of this macroevolutionary dichotomy can be suggested; however, it could be obtained from extrinsic information such as the age of the biogeographical pattern of which these fishes are a part (Humphries & Parenti, in press).

The phyletic affinity of the expanded Synbranchiformes remains uncertain. Berg (1940) suggested a possible relationship between ophicephalids and synbranchids and Travers (1981) noted their possible affinity with the carapids (Ophidiformes: Cohen & Nielson, 1978); a group which, in common with the synbranchids, have a massive ectopterygoid associated with the absence or fusion of the endopterygoid. A comparison between these groups should be the subject of future investigation.

Mastacembeloid intrarelationships

Incorporated in the following analysis are numerous reductional features and absences which are common in several mastacembeloid lineages, particularly those with a small adult size. Features of this type are of doubtful value to phylogenetic analysis when considered individually because they are inclined to occur independently (i.e. convergently) in closely related lineages. However, if two taxa share a unique set of uncorrelated reductional characters, in combination they are reliable evidence (synapomorphies) in support of a monophyletic origin of the group. By necessity, such character sets form a substantial part of this analysis and are discussed in detail below.

I. Character analysis

Osteology

NEUROCRANIUM

In general the mastacembeloid orbital region is characterised by the presence of large pterosphenoids and by their ventromedial connection (Travers, 1984: 14). Although this is the condition in the majority of taxa, the pterosphenoid can occur in two other states. In *Mastacembelus aviceps* (Travers, 1984: fig. 40) the bone is a small splinter-like element sutured along the dorsolateral edge of the frontal. The neurocranium in this microphthalmic species is very small, with many apparently reductional features (discussed below). The condition of the pterosphenoid in *M. aviceps* is intermediate between that in the majority of mastacembeloids and that in *Chaudhuria* and *Pillaia* where it is absent. The secondary loss (i.e. ontogenetic suppression) of the pterosphenoid in *Chaudhuria* and *Pillaia* is a useful synapomorphy of these taxa. The splinter-like pterosphenoid is an autapomorphy of *M. aviceps,* and it may be under similar developmental influences to those which have culminated in the complete loss of the pterosphenoid in *Chaudhuria* and *Pillaia*.

The basisphenoid, too, is absent in *Chaudhuria* and *Pillaia* (Travers, 1984: 53). The lack of a basisphenoid in *Mastacembelus aviceps* and *Mastacembelus crassus* seemingly parallels the condition in *Chaudhuria* and *Pillaia,* and is one of several other parallelisms (discussed below) found only in these taxa among the mastacembeloids I have examined.

A divided posterior end of the parasphenoid is the plesiomorphic condition and occurs in most groups of teleostean fishes. The absence of these processes in the beryciforms (the posterior end of the parasphenoid tapers to a single point along the ventral surface of the basioccipital; Zehren, 1979: 50) appears to be an apomorphic condition.

The basal perciforms ('lower percoids' of Greenwood *et al.*, 1966) typically have the posterior end of the parasphenoid divided into a pair of processes and this is the arrangement in representatives of most perciform groups, including the mastacembeloids.

The basicranium of *Mastacembelus congicus* illustrated by Rosen & Greenwood (1976: fig. 57) inaccurately depicts the posteroventral edge of the parasphenoid as undivided (i.e. in an apomorph condition). The posteroventral region of the parasphenoid in specimens of *M. congicus* is divided into a pair of processes and is similar in this respect to most other mastacembeloid taxa (Travers, 1984: 14).

However, in a number of mastacembeloids the parasphenoid is undivided except for its posterior tip (Travers, 1984: 53). In *Macrognathus* species, *Mastacembelus pancalus* and *Mastacembelus zebrinus* (species F–J in the cladogram Fig. 19 and possibly some or all from the species in the unresolved polychotomy E) the posteroventral face of the parasphenoid is excavated into a blind pit divided medially by a longitudinal ridge. Associated with the deep basicranium in these taxa is a deep exoccipital which has an exceptionally wide ventrolateral face. The deep basicranium with a pitted ventral surface is unique to these mastacembeloids, and is considered to be a synapomorphy uniting this species complex (E–J in cladogram). The fossa accommodating the anterior end of Baudelot's ligament on the posteroventral corner of the basioccipital (Travers, 1984: 70) is particularly deep in these species.

The posterior parashenoid processes in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* are exceptionally long and extend from the region of the parasphenoid adjacent to the lateral commissure to beyond the posterior margin of the basioccipital (Travers, 1984: 53). The relative length of these processes far exceeds that in any other mastacembeloids, and in perciform lineages generally, and is a synapomorphy uniting *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (species complex A–C in the cladogram).

An anterior process on the prootic extending unopposed into the orbital cavity, is a synapomorphy of the mastacembeloids. The anterior process (see p. 91) is absent in *Pillaia, Mastacembelus aviceps* and *Mastacembelus crassus,* giving the bone in these taxa the appearance of the plesiomorphic type. However, the reduced crania (including the loss and reduction of many bones) in these microphthalmic species and their small adult size appear to be indicative of a highly derived state. Thus, the lack of a prootic process would be a secondary loss (i.e. an evolutionary reduction or reversal) rather than a primary absence and one of many such 'apomorphic' losses in these taxa.

The comparatively simple pars jugularis in mastacembeloids is typical of advanced teleosts (p. 91). Among the mastacembeloids a single foramen in the pars jugularis is found only in *Chaudhuria*, *Pillaia* and *Mastacembelus crassus* (Travers, 1984: 67) and is another 'apomorphic reduction' shared by these taxa.

The trigeminal foramen in many mastacembeloids is bordered anteroventrally by a small pedicel that rises from the dorsal edge of the prootic (Travers, 1984: 64). This spur is homologous with a prootic process connected to the tip of a descending pterosphenoid pedicel, anterior to the pars jugularis, in other teleosts (e.g. the 'internal jugular bridge' in labroids; see Rognes, 1973: 69).

The development of this structure has been discussed in detail by Greenwood (1976: 20–27) with respect to its occurrence in the centropomids. Greenwood (1976) found the internal jugular bridge to have a mosaic occurrence among living teleosts, particularly in those with precommissural elongation of the neurocranium. He also showed that the relative contribution of the prootic, pterosphenoid and parasphenoid to the formation of an internal jugular bridge is prone to marked intraspecific variation in *Lates*, and that the pterosphenoid pedicel, or at least the potential to develop it, is primitive for actinopterygians.

Based on this, and the fact that a pterosphenoid pedicel is an integral part of the internal jugular bridge, Greenwood (1976: 27) concluded '. . . that the bridge too is a primitive feature'.

If an ascending spur is present on the prootic in *Lates* and the other teleosts Greenwood examined it always contributes to the bridge. A prootic ascending spur is present in the majority of mastacembeloids, yet in none does it contribute to the formation of a bridge. This appears to be related to the extreme precomissural elongation of the skull in these fishes (Travers, 1984: fig. 1a to c), and the position of the prootic spur (posterior to the pterosphenoid).

In several mastacembeloids, however, the vessels emerging from the trigeminal foramen are bridged by a type of internal jugular bridge formed by the tip of the prootic anterior process curving anterodorsally (functionally replacing the prootic ascending spur in this respect) and contacting a prominent descending pedicel on the frontal (e.g. *Mastacembelus paucispinis* and *Mastacembelus moorii*; Travers, 1984: 60). In the new species of *Mastacembelus* (Roberts & Travers, in prep.) a narrow ligament runs from the anterior tip of the prootic to the ventral edge of a weakly developed frontal pedicel in much the same manner as the internal jugular bridge ligament described by Greenwood (1976: 22).

The type of prootic/frontal internal jugular bridge occurring in mastacembeloids is not found in any other teleost, which suggests that it is an apomorphic development in these taxa, and possibly a synapomorphy of *M. moorii, M. paucispinis* and *M. sp. nov.*

Apart from these species, an internal jugular bridge type structure was found in *Mastacembelus albomaculatus, M. plagiostomus, M. tanganicae* and *M. congicus*. In these species the bridge may be formed by a pterosphenoid pedicel or by the prootic process alone (Travers, 1984: 60).

Those mastacembeloids in which the prootic ascending spur is reduced or absent from the rim of the trigeminal foramen may be interpreted as exhibiting an apomorphic condition relative to that in which a prominent spur is present. The relatively posterior position of the spur in mastacembeloids indicates that the main region of neurocranial lengthening has been anterior to the lateral commissure (i.e. between the prootic spur and the posterior edge of the orbit) in these fishes.

An extension of the prootic (anterodorsal to the lateral commissure) occurs along the ventral edge of the sphenotic in *Macrognathus* species (Travers, 1984: 68). This flange on the prootic distinguishes these taxa from other mastacembeloids. It borders the upper rim of the trigeminal foramen (to a variable extent); in its most developed state (i.e. *Macrognathus aculeatus*; Travers, 1984: fig. 30a) the flange forms the entire upper rim of the trigeminal foramen. A sequential change in the size of the prootic flange occurs in *Macrognathus aral* and *Macrognathus siamensis,* so that in its least well developed condition it borders only the most posterodorsal margin of the foramen. The presence of this flange is an apomorphic character of *Macrognathus* and is found in a specific state in each of the three *Macrognathus* species.

The saccular otolith in *Mastacembelus brichardi, M. crassus* and *M. aviceps* (Travers, 1984: figs. 39 & 40) is large in relation to that in other mastacembeloids, and is housed in a correspondingly large bullation of the prootic. The large bulla of *M. brichardi, M. crassus* and *M. aviceps* (Travers, 1984: figs. 38–40) is most probably synapomorphic for these species (P, R & S; and possibly *M. latens* [Q], for which no material was available).

The saccular bullae in *Chaudhuria* and *Pillaia* are exceptionally large, with the bulla contained in approximately equal parts in the prootic, exoccipital and basioccipital (Travers, 1984: fig. 15 ai & bi). This arrangement in *Chaudhuria* and *Pillaia* appears to be the plesiomorphic condition (as described in Travers, 1984: 69), but should, perhaps, be interpreted as a redevelopment of the primitive condition (see p. 133 for discussion of reductional trends and 'plesiomorphic mimicry').

In only one of the African taxa, *Mastascembelus micropectus* (a microphthalmic species from Lake Tanganyika; Travers, 1984: fig. 38d), is the large saccular bulla contained in approximately equal parts of the prootic, exoccipital and basioccipital bones.

The dorsal surface of the exoccipital is perforated in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (Travers, 1984: 69). Although foramina may occur in other mastacembeloids, in none is there the dense perforations typical of these taxa. In addition, the posterior tip of the supraoccipital in *M. sinensis, Chaudhuria* and *Pillaia* separates the dorsomedial margin of the exoccipital from contacting its partner in the midline.

The fact that the exoccipitals in all other mastacembeloids lack a perforated dorsal surface suggests that this character is an apomorphic development in *M. sinensis, Chaudhuria* and *Pillaia.* The posterior extension of the supraoccipital associated with this perforation is an additional synapomorphy uniting these taxa (complex A–C) and is an apomorphy congruent with the very long posterior parasphenoid processes (see. p. 111).

A group of Asian taxa comprising the *Macrognathus* species, *Mastacembelus pancalus* and *M. zebrinus* (and possibly some or all of the species included in polychotomy E) are distinguished from all other mastacembeloids by the steeply sloping dorsal surface of the frontals and extremely narrow neurocrania. Among the examined species showing this trend, it is best developed in *Mastacembelus pancalus* (Travers, 1984: fig. 28a). On account of this and of several other features (e.g. fin length, caudal skeleton and the ratio between the number of abdominal and caudal vertebrae), *M. pancalus* is thought to be the most highly modified of these species. The deeply sloping frontals in *Macrognathus, M. pancalus* and *M. zebrinus* (and possibly some or all species of category E) are a synapomorphy uniting the group.

The frontals in *Chaudhuria* and *Pillaia* (Travers, 1984: 72) lack a descending lamina, another apparently reductional character in these taxa, which does not occur in any other mastacembeloids.

The anterior region of the frontal, roofing the orbital cavity, is reduced in *Mastacembelus brichardi, M. crassus* and *M. aviceps* (p. 138); it is short compared with that in most species. This size reduction in the orbital region of the frontals is a synapomorphic character of these species and one apparently associated with their tendency to be micro- and cryptophthalmic.

In all mastacembeloids apart from *Mastacembelus sinensis* (Travers, 1984: 71), the parietals are separated in the midline by the supraoccipital. The short supraoccipital in this species may not restrict the medial edges of the parietals from contacting one another anteriorly although in some individuals this restriction did occur. Complete medial interparietal contact is a plesiomorphic characteristic of the teleosts (Forey, 1973: 187), and is of wide occurrence. With the exception of the synbranchids (Rosen & Greenwood, 1976), the percomorphs have their parietals separated in the midline by the supraoccipital. It is, thus unlikely that the slight anteromedial parietal contact that may occur in some *M. sinensis* individuals should be interpreted as a plesiomorphic condition. The medial contact of the parietals in *M. sinensis,* is possibly associated with the small size of the supraoccipital in this species.

The cephalic sensory canal system is well developed in all mastacembeloids apart from *Chaudhuria* and *Pillaia.* In *Pillaia* (Travers, 1984: 45) the sensory canals are present, incompletely, in the preoperculum, dentary, frontal, 1st infraorbital and nasal bones, while in *Chaudhuria* (Travers, 1984: 36) they are absent from all cranial bones. The reduction and loss of these canals in *Chaudhuria* and *Pillaia,* appears to represent another synapomorphic secondary loss and part of the evolutionary reduction that characterises these taxa.

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The upper jaw is composed of a single bone in *Pillaia* (Travers, 1984: fig. 16b), and its shape suggests that it incorporates the premaxilla and the maxilla (Yazdani, 1976). The anterior region of the maxilla in *Mastacembelus aviceps* (Travers, 1984: fig. 44a) is greatly reduced and is tightly connected to the dorsal surface of the premaxilla. This arrangement may serve to illustrate the method by which the pillaiid condition (fused single element) was brought about (see Travers, 1984: 75).

A single upper jaw element was found only in *Anguilla* amongst the outgroups examined. Here, however, the upper jaw is partly fused with the cranium; the maxilla and premaxilla-ethmovomerine bloc having taken over its function (Norman, 1926).

The close association between the maxilla and premaxilla in *M. aviceps* and the fusion between these elements in *Pillaia* are derived modifications autapomorphic for these species.

The size of the premaxillary alveolar surface and the number of teeth it supports vary greatly among mastacembeloids. The premaxillary dentition typical for most taxa consists of an outer row of large caniniform teeth followed by 3 or 4 medial rows decreasing in tooth number and size posteriorly (see Travers, 1984: 76).

Two major modifications of this plesiomorph condition can be recognised. A narrow alveolar surface with only 1–2 inner tooth rows occurs in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* and may be a synapomorphy of these taxa. Conversely the premaxillary alveolar surface is expanded in an assemblage of Asian taxa (Travers, 1984: 76) which includes all *Macrognathus* species, *Mastacembelus pancalus* and *Mastacembelus zebrinus* (and perhaps some or all of the species in lineage E of Fig. 19). In these taxa the alveolar surface extends anterolaterally well beyond the premaxilla and develops a toothed vertical face, the like of which has not been observed in any other teleosts. In other mastacembeloids, as in teleosts generally, an increase in size of the upper jaw dentition always involves the medial expansion of the alveolar surface along its inner edge (as seen in *Mastacembelus moorii*; Travers, 1984: 76) to produce a broad vertical surface toothed on its medial face. Clearly the development of a vertical, anterolaterally extended, premaxillary tooth face is a shared, derived feature of the mastacembeloid taxa in which it is manifest.

In some instances it leads to the development of a series of toothplates which extend along the ventral surface of the large rostral appendage (Travers, 1984: fig. 45b & c), a condition unique to the mastacembeloids and a synapomorphy of those species at present combined generically, mainly because of this feature, in *Macrognathus*. This character can be subdivided into three states each represented by one of the three *Macrognathus* species: *Macrognathus siamensis* has 7–14 rostral toothplates; *M. aral* 14–28, and *M. aculeatus* 38–55 (Roberts, 1980).

There is a distinct morphocline in the anterolateral expansion of the premaxillary alveolar surface ranging from the relatively narrow one in *Mastacembelus keithi* (part of polychotomy E), to the broad surface with numerous (over 50) fragmented rostral toothplates in *Macrognathus aculeatus*.

The posteroventral extension of the dentary below the anguloarticular is a synapomorphy of the mastacembeloids (p. 98). In *Chaudhuria* the ventral edge of the dentary is forked giving rise to a distinctive pair of posteroventral processes (Travers, 1984: 36). This autopomorphic characteristic of *Chaudhuria* distinguishes it from *Pillaia,* with which it shares many apparently synapomorphic features.

The coronoid process on the dentary has been shown to occur in two major conditions, either tall and narrow or short and broad (Travers, 1984: 80). Based on the condition of their coronoid process, the mastacembeloids fall into two major assemblages. These groups, however, are incongruent with the lineages (see Fig. 19) revealed by numerous characters recognized in this study. A parsimonious explanation of this incongruence in the condition of the coronoid processes is suggested by the direct correlation between them and the feeding strategy employed, particularly since the demands of feeding are thought to impose the highest stresses on the cephalic structures of predatory fishes (Osse & Muller, 1980).

Liem (1967) has shown that in the luciocephaloid *Luciocephalus pulcher* the strength of the 'bite', a result of contraction of part A_2 of the *adductor mandibulae*, is enhanced by the height of the ascending (coronoid) process of the dentary. More recently, teleostean modes of feeding have been divided into three major categories (Liem, 1980b) and 'biting' is now considered to be part of the broad, more general feeding strategy of manipulation. The great length of the ascending process on the dentary in *Luciocephalus* increases the torque about the jaw articulation, thereby, providing the greatest mechanical advantage for manipulating prey. This gives a clue to the variation in size of the mastacembeloid coronoid process, particularly as it is short (low/broad) in taxa which have reduced upper jaw bones (e.g. *Macrognathus* species); associated with expansion of the toothbearing alveolar surface, a relatively small A_2 muscle and increased size of the anterior region of the *adductor arcus palatini.* The diet of aquatic insect larvae and oligochaetes (Roberts, 1980) in *Macrognathus* is that expected in fishes with a weak 'bite'. Conversely, those mastacembeloids with a large upper jaw bone (and medially expanded alveolar surfaces), a high (tall/narrow) coronoid process and a well-developed A_2 muscle (e.g. *Mastacembelus mastacembelus* and *Mastacembelus moorii*), are generally predatory piscivores which need a 'bite' of greater strength than do the insectivores.

The length of the coronomeckelian in mastacembeloids has been found to be inversely proportional to the height of the coronoid process on the dentary (Travers, 1984: 81). If coronomeckelian length can be taken as a measure of the size of the A_3 part of the *adductor* *mandibulae* (see Travers, 1984: 125), it may reflect the change in emphasis on particular parts of the adductor musculature with regard to the feeding strategies employed. In species which are principally insectivorous (e.g. *Macrognathus*) and have a relatively weak 'bite' there is a greatly developed coronomeckelian and A_3 part of the *adductor mandibulae*. The size and the strength of these elements may help to increase the efficiency of the high speed inertial suction mode of feeding probably employed by such fishes when capturing small prey or food. In contrast, when mastacembeloids capture large prey or food items (i.e. predaceous piscivores such as *M. mastacembelus* and *M. moorii*) they firmly grasp and bite the prey until it is rendered (by being broken down to a smaller size and/or correctly positioned) to a state which, with the aid of inertial suction, can be readily engulfed. The initial manipulation of large prey or food requires a 'bite' of greater strength (produced by the larger height—tall/narrow—of the coronoid process and relatively great size of part A_2) for grasping and biting, and places less reliance on inertial suction as the major mode of feeding, thus obviating to some extent the need for a very long coronomeckelian and a well-developed A_3 *adductor mandibulae* muscle.

A group of taxa with a low/broad coronoid process may be distinguished by the posterior encroachment of the toothbearing alveolar surface on the dentary, across the medial face of the coronoid process (Travers, 1984: 80). This development is considered to be apomorphic, as no outgroup taxa had a toothed medial face of the coronoid process. It is another synapomorphy of the Asian mastacembeloid lineage comprising the *Macrognathus* species, *M. pancalus* and *M. zebrinus* (and possibly some or all of those species in polychotomy E of Fig. 19), and is evidence in support of the monophyletic origin of this Asian lineage since it is congruent with similar indications provided by the anterior expansion of the premaxillary alveolar surface (see above p. 114).

A large, dorsally situated coronomeckelian is a synapomorphy uniting most mastacembeloids. However, in *Chaudhuria* and *Pillaia* (Travers, 1984: 80) it is a small ossicle on the medial face of the anguloarticular, posterodorsal to Meckel's cartilage, and resembles the plesiomorphic condition seen in such groups as the percoids.

The variable size of the coronomeckelian in all other mastacembeloid taxa has been functionally related to the size of the coronoid process on the dentary (p. 114). The small coronomeckelian in *Mastacembelus brachyrhinus, M. brichardi, M. aviceps* and *M. crassus* (and possibly *M. latens* as well—species O to S in cladogram), however, is much smaller than would be expected from the height of the coronoid processes in these taxa. The condition is exceptional among mastacembeloids, and rather than being related to the jaw mechanism (e.g. height of coronoid process) would appear to be governed by the reductional trend characterizing many other features of their anatomy, and is presumably another synapomorphy uniting these species. However, even in its reduced state it represents a condition that is derived relative to that in the outgroup taxa examined.

The condition of the coronomeckelian in *Chaudhuria* and *Pillaia,* which also demonstrate several reductional features could be truly plesiomorphic. However, this explanation is less parsimonious than the alternative view that, the coronomeckelian in *Chaudhuria* and *Pillaia* has been secondarily reduced.

The absence of a coronoid process on the anguloarticular in the majority of mastacembeloids has been discussed in the previous section (p. 99), and is a plesiomorphic feature. The low, broad-based coronoid projection on the anguloarticular in *Mastacembelus zebrinus, M. pancalus* and all *Macrognathus* species, thus distinguishes them from all other mastacembeloids. Its development in these species is considered to be derived in a manner similar to that described by Rosen & Greenwood (1976: 46) for a coronoid process on the anguloarticular in two synbranchid taxa.

Macrognathus is also distinguished from all other mastacembeloids by the anterior position of the facet that notches the dorsal edge of the anguloarticular (Travers, 1984: 82). In all other species the facet occurs on the posterodorsal edge of the bone. Although the position of the facet is subject to variation amongst the percomorphs, it generally lies on the posterodorsal edge of the anguloarticular, especially if there is a large coronoid projection. The position of the facet in *Macrognathus* is, therefore, considered to be an apomorphic feature.

THE PTERYGO-PALATINE ARCH

In most mastacembeloids the metapterygoid is widely separated from the anteroventral edge of the hyomandibula. The symplectic in these taxa is a long bone which often has an irregular dorsal lamina whose upper edge contacts the ventral edge of the metapterygoid (Travers, 1984: 82).

In *Mastacembelus sinensis, Chaudhuria* and *Pillaia,* however, the symplectic is smaller than in most other mastacembeloids, and the metapterygoid and hyomandibula are in contact.

Of these two conditions, the latter is the more common being widely found among higher neoteleostean fishes, occurring even in those which have a large symplectic (e.g. *Ophidion rochei* and *Carapus acus,* Fig. 14a; *Congrogadus subduceus,* Fig. 9; *Notothenia sema,* Fig. 14b; *Eliotriodes sexguttatus,* Fig. 14c; *Luciocephalus pulcher,* Fig. 14d).

Thus, the contact between the hyomandibula and metapterygoid in *M. sinensis, Chaudhuria* and *Pillaia* more closely approximates to the arrangement of these bones in other neoteleosts than does the wide separation of the hyomandibula and metapterygoid characteristic of the other mastacembeloid taxa. On this basis the arrangement in *M. sinensis, Chaudhuria* and *Pillaia* is thought to represent the plesiomorphic condition, (alternatively, it could be a secondary redevelopment that simply mimics it), whilst the wide separation between these bones is a synapomorphy of all other mastacembeloids (the Asian and the African species D–S in Fig. 19).

The size and shape of the endopterygoid is highly variable among neoteleosts, and the bone may even be absent.

The mastacembeloid endopterygoid also varies in shape and size (Travers, 1984: 83) but generally it lies dorsal to the quadrate, its anterior end overlying the posterodorsal edge of the ectoperygoid, and its posterior end overlapping the anterodorsal edge of the metapterygoid. The posterior end of the endopterygoid is often subdivided into blunt, posteromedially directed processes. Fibres of the *adductor arcus palatini* muscle merge into short tendons which insert on the tips of these processes. Since this state most closely resembles that in other percomorph lineages, it is thought to represent the plesiomorphic condition of the mastacembeloids.

A boomerang-shaped endopterygoid occurs in a group of Asian mastacembeloids including *Mastacembelus mastacembelus, M. armatus, M. erythrotaenia, M. oatesii, M. unicolor* and possibly *Mastacembelus alboguttatus* (for which no material was available), i.e. the species forming D in cladogram. The posterior arm of the endopterygoid in these species has an undivided tip that extends across the quadrate/metapterygoid junction; the anterior arm is larger than the posterior arm, and extends between the ectopterygoid/lateral ethmoid point of articulation. The anterior elongation of the endopterygoid is an apomorphic development, and provides a synapomorphy uniting *M. mastacembelus, M. armatus, M. erythrotaenia, M. oatesii, M. unicolor* and possibly *M. alboguttatus.*

A very small splinter-like endopterygoid is a characteristic feature of the suspensorium in *Mastacembelus brichardi, M. aviceps, M. crassus* and probably in *M. latens* (Travers, 1984: 83). The small size of the bone may be a secondary reduction and would, in that case, be a synapomorphic character uniting these species (species P–S in Fig. 19). The absence of an endopterygoid in *Mastacembelus sinensis, Chaudhuria* and *Pillaia,* may be the culmination of this trend, in which case it is a synapomorphy for these taxa.

In *Chaudhuria* and *Pillaia* no palatine could be identified and it may be fused with the ectopterygoid, a fusion which could account for the particularly long anterodorsal arm of the ectopterygoid in these species (Travers, 1984: fig. 17a & b).

The medial face of this long anterior arm does not articulate with the lateral ethmoid in *Chaudhuria* and *Pillaia.* Instead, it lies along the posterolateral face of the vomerine shaft. The narrow lateral face of the ectopterygoid, its long anterodorsal arm connected to the

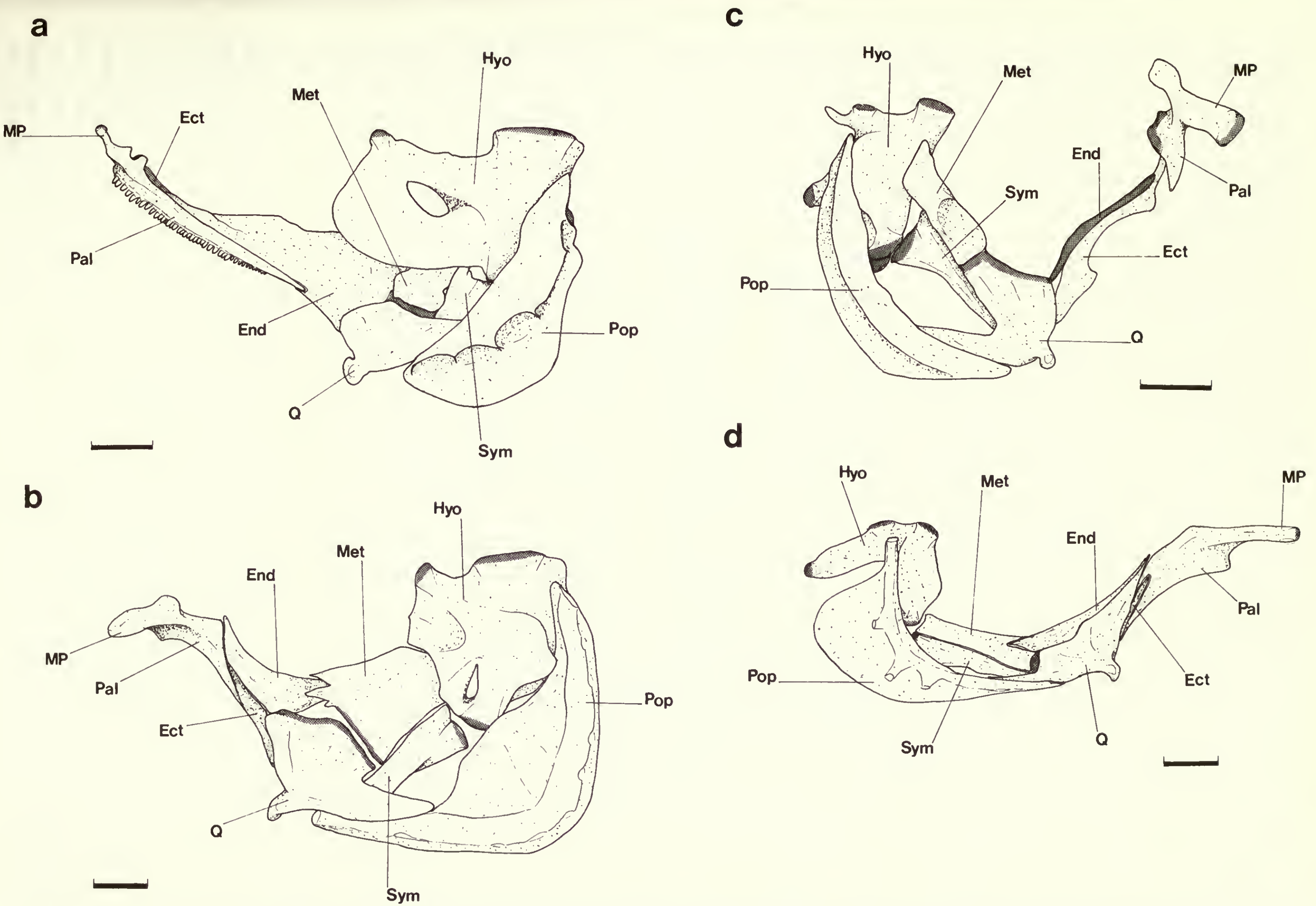

Fig. 14 Lateral view: left hyopalatine arch and preoperculum in (a) *Carapus acus* and (b) *Notothenia sema*; right hyopalatine arch and preoperculum in (c) *Eleotriodes sexguttatus* and (d) *Luciocephalus pulcher*.

vomerine shaft, and the loss (or fusion) of the palatine, are all synapomorphic characters uniting *Chaudhuria* and *Pillaia*.

The relatively narrow lateral face and long anterodorsal arm of the ectopterygoid in *M. sinensis*, would seem to represent an intermediate stage of character transformation between that found in the majority of mastacembeloids and that in *Chaudhuria* and *Pillaia*. The small size of the palatine, which does not extend posteriorly into the orbital cavity in *M. sinensis*, also appears to be an intermediate condition between the two groups. Although the lack of a deep anterolateral face on the ectopterygoid in *M. sinensis, Chaudhuria* and *Pillaia* may be plesiomorphic (relative to the usual mastacembeloid condition), associated as it is with the loss of direct articulation between the lateral ethmoid and the palatine, it is considered to be derived, through reduction from that in the majority of mastacembeloids. Thus, it too is a synapomorphy for the three taxa.

An ectopterygoid with a narrow lateral face (relative to that in the majority of species), but lacking a great increase in the length of its dorsal arm and reduction or loss of the palatine, occurs in *Mastacembelus aviceps, M. crassus* and possibly *M. latens*. The small lateral face of the ectopterygoid in these species could be at an intermediate stage in the reductional trend culminating in the condition seen in *Chaudhuria* and *Pillaia*. If this is the case it is a synapomorphy uniting *M. aviceps* and *M. crassus* (R & S in Fig. 19).

The anterior edge of the quadrate is approximately straight in the majority of the mastacembeloids (Travers, 1984: 83). In *Macrognathus, Mastacembelus pancalus* and *M. zebrinus* (and possibly part or all of polychotomy E) it is deeply indented across the particularly large posteromedial processes on the ectopterygoid. This indentation of the quadrate is considered to be a synapomorphy for these species (F–J in Fig. 19).

A round facet on the posteromedial margin of the ectopterygoid articulates with a similar facet on the anterolateral margin of the quadrate in *Mastacembelus pancalus* (Travers, 1984: 83). An articulatory facet between these bones is not found in any other mastacembeloids, and is thus an autapomorphy which may be associated with the very deep anterolateral face of the ectopterygoid in *M. pancalus*.

A small and weak ascending spur present on the palatine in the majority of mastacembeloids is the only remnant of the plesiomorph condition in which the bone is connected to the lateral ethmoid (see discussion on p. 102). In some Oriental species (*Macrognathus* species, *Mastacembelus pancalus* and *M. maculatus*) even this spur is absent, a condition representing the culmination of a trend in mastacembeloids leading to the complete loss of the palatine (as in *Chaudhuria* and *Pillaia*). The loss of the palatine spur also occurs, mosaically, among the African mastacembeloids (see Travers, 1984: 86) and must be considered a trend independent of that in *Macrognathus, Mastacembelus pancalus* and *M. maculatus*. Thus, its loss is treated in each instance as an apomorphic feature, and one that appears to have occurred independently on several occasions. If the lack of the spur in *Macrognathus* species and *Mastacembelus pancalus* is considered as a synapomorphy of these taxa, it adds support to two other synapomorphies (discussed below—see p. 118 & 123) that unite them.

OPERCULAR SERIES

The lateral face of the mastacembeloid preoperculum is pierced by 4 or 5 sensory canal pores in the majority of taxa (Travers, 1984: 86). Five preopercular sensory canal pores occur commonly among many perciform assemblages, including the blennioids, gobioids and a variety of percoid families, for example pseudochromids (*sensu* Springer, Smith & Fraser, 1977), percoids, cichlids and cepolids; this most probably represents the plesiomorphic condition. A decrease in the number of these pores, therefore, is an apomorphic tendency.

Such an apomorphy is found among certain mastacembeloids (Travers, 1984: 86), including an assemblage of at least 13 African species (the polychotomous species complex L) as well as in species M–S (see Fig. 19).

A reduction in the number of pores is carried to an even greater extreme among what appears to be a sublineage of the assemblage containing the polychotomy L and species M to S. In the latter there is a sequential loss of sensory canal pores from 5 in *Mastacembelus paucispinis* and the undescribed *Mastacembelus* species (the model number for the assemblage containing both polychotomy L and species M to S) to 4 in *Mastacembelus brichardi,* 3 in *Mastacembelus brachyrhinus,* and finally 2 in *Mastacembelus crassus* and *Mastacembelus aviceps* (Travers, 1984: fig 44a & b). If loss of preoperculum sensory canal pores is considered as a synapomorphy which can occur in several states (i.e. 4, 3 or even 2 pores) each of which is apomorphic for a particular species, the trend could be cited as evidence supporting a monophyletic origin for the species in which it occurs. This hypothesis is also supported by a similar sequential decrease in the number of caudal vertebrate in *Mastacembelus paucispinis,* the undescribed *Mastacembelus* species, *M. brachyrhinus, M. brichardi, M. aviceps* and *M. crassus* (see p. 126), and by the absence of a toothplate on hypobranchial 3 in these species (discussed on p. 124).

Five preopercular pores generally are present in the majority of the other African species (the ill-defined complex K in Fig. 19). However, 7 species in this complex have 4 pores (see Travers, 1984: 86) and, on the basis of this character, these species should be more closely related to species in polychotomy L and to species M to S than to other members of complex K.

So far no character has been found to unravel the interrelationships of the 4–pored species tentatively included in complex K. There are, however, a number of synapomorphies (not found in complex K) which unite the species included in the assemblage comprising polychotomy L and species M to S. Thus, for the time being, the presence of only 4 preopercular sensory canal pores in certain members of complex K must be considered an independently acquired character.

The upper preopercular sensory canal in *Mastacembelus crassus* and *M. aviceps,* instead of opening at the dorsal tip of the preoperculum, opens along its posterodorsal edge. This positioning of the preopercular canal was not found in any outgroup taxa and is considered to be synapomorphic for these species.

In *Macrognathus* and in *Mastacembelus pancalus* the three central pores open from the tip of short, descending branches of the main preopercular canal (Travers, 1984: fig. 45b & c). This branching of the canal is probably correlated with the wide lateral face of the preoperculum in these taxa. In representatives from a number of perciform lineages including the percoids (e.g. the cichlids *Astatotilapia burtoni* and *Crenicichla alta* and to a lesser extent the pseudochromid *Pseudochromis caudalis*) the preopercular sensory canal may also be branched. This independent development of a branched sensory canal appears, in each instance, to be an apomorphic feature. Its development in *Macrognathus* and *M. pancalus* alone amongst mastacembeloids strongly suggests that it is a synapomorphic feature for these two taxa and may be used as further evidence in support of the view, proposed earlier, on the basis of other features (p. 118), that *M. pancalus* is more closely related to *Macrognathus* than to any other mastacembeloid.

HYOID AND BRANCHIAL ARCHES

The anterior ceratohyal is connected to the posterior ceratohyal by a series of interdigitating dentate sutures in all mastacembeloids, apart from *Chaudhuria* and *Pillaia* (Travers, 1984: 87). In *Mastacembelus sinensis* these processes are relatively short, irregularly positioned spikes (Travers, 1984: fig. 51) that extend into the cartilaginous interface only. A single flange extends from the anterior to the posterior ceratohyal in *Chaudhuria* and *Pillaia* (Travers, 1982: fig. 19a & b) but otherwise the bones are connected by a straight cartilaginous suture.

A straight suture is the arrangement found in most teleosts below the acanthomorph level I have examined. The development of interdigitating dentate processes connecting the two ceratohyals occurs mosaically among phyletically diverse higher acanthomorph lineages and even among closely related taxa. For example, among the illustrations of various paracanthopterygian hyoid arches shown by Rosen & Patterson (1969), in only one batrachoid species (*Thalassophryne megalops*; fig. 57a) are the anterior and posterior ceratohyal shown as connected by interdigitating processes. More recently, Zehren (1979) has described the osteology of nine beryciform families and in only one—Berycidae—are the ceratohyals connected by interdigitating processes. Among the percoids there is considerable variation in the way the ceratohyals are interconnected. This is shown by MacDonald (1978) in the Percichthyidae; in some (e.g. *Maccullochela peeli*) there is a large interdigitating process whilst in others (e.g. *Macquaria australasia*) the connection is by a straight suture. A similar situation is shown in different nandid genera by Liem (1970). The centropomids on the other hand, when viewed laterally, have a straight suture (as illustrated by Greenwood, 1976: fig. 20), but in medial view a number of small interdigitating processes can be seen.

In the synbranchids (Rosen & Greenwood, 1976: figs. 25 & 42 to 50) the ceratohyals are always connected by large dentate sutures.

Although the development of (or at least potential to develop) interdigitating ceratohyal processes is apomorphic for acanthomorph fishes, the mosaic distribution of this character makes it of limited taxonomic value.

The arrangement of the anterior and posterior ceratohyal in *M. sinensis, Chaudhuria* and *Pillaia* resembles, to some extent, the plesiomorphic condition but it is most probably a result of the interdigitating process having been secondarily lost and may be considered as a further synapomorphy of these highly derived taxa.

Basibranchial 1 in mastacembeloids has a deep ventral keel in all taxa except *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (Travers, 1984: 90). An outgroup survey of this character reveals that it has a similar mosaic distribution to that of the ceratohyal suture described above. For example, a keel of relatively small proportions (compared with that

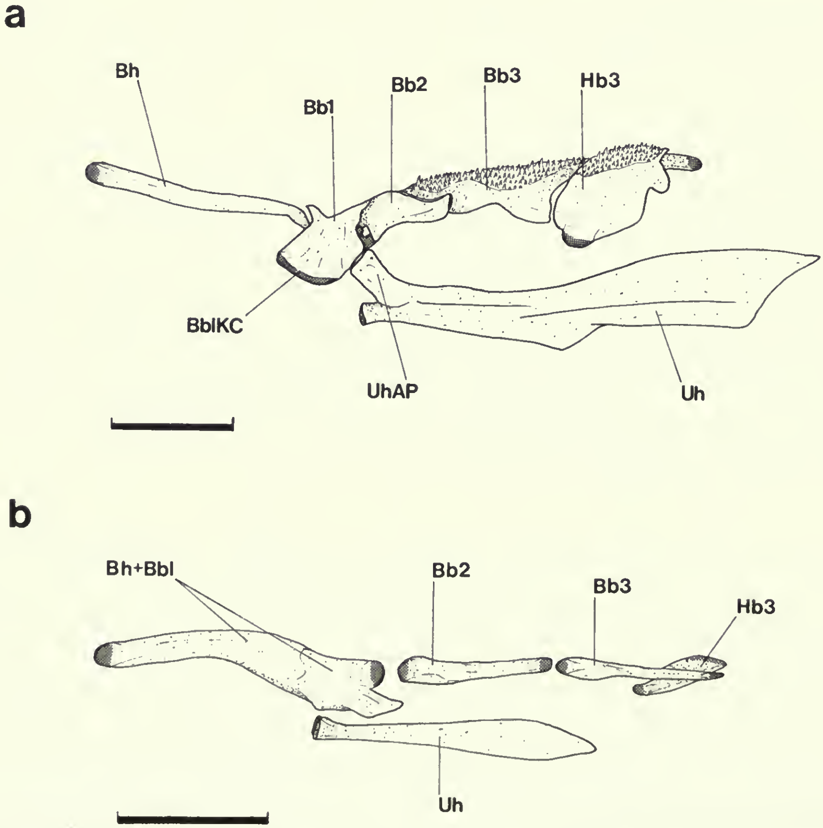

Fig. 15 Basibranchial/urohyal arrangement in: (a) *Carapus acus*; (b) *Synbranchus marmoratus*, lateral aspect, left side.

in the mastacembeloids) occurs on basibranchial 1 in the ophidioids (e.g. *Carapus acus* Fig. 15a); the synbranchids have a well developed keel that extends posteriorly below the anteroventral surface of basibranchial 2 in most taxa (e.g. *Synbranchus marmoratus* Fig. 15b), as do many perciforms, although it is low in sphyraenoids, trachinoids, anabantoids and channoids.

The flat ventral surface of basibranchial 1 in *M. sinensis, Chaudhuria* and *Pillaia* resembles the plesiomorphic condition, and could be either primarily plesiomorphic or a secondary redevelopment of that condition. The arrangement of the keel in *Mastacembelus aviceps* and *Mastacembelus crassus* (Travers, 1984: fig. 55) may help to resolve this problem. In these species, although the keel is present, it is much smaller than that in the other mastacembeloids. On the basis of many other characters, *M. aviceps* and *M. crassus* can be considered highly derived species exhibiting several features in a somewhat reduced state and intermediate between the modal condition and that in *Chaudhuria* and *Pillaia*. The low keel on basibranchial 1 in *M. aviceps* and *M. crassus* may be such a character. If, during evolution, reduction of the keel has occurred in these mastacembeloids, the arrangement of the keel in *M. sinensis, Chaudhuria* and *Pillaia* could well be the result of a similar trend,

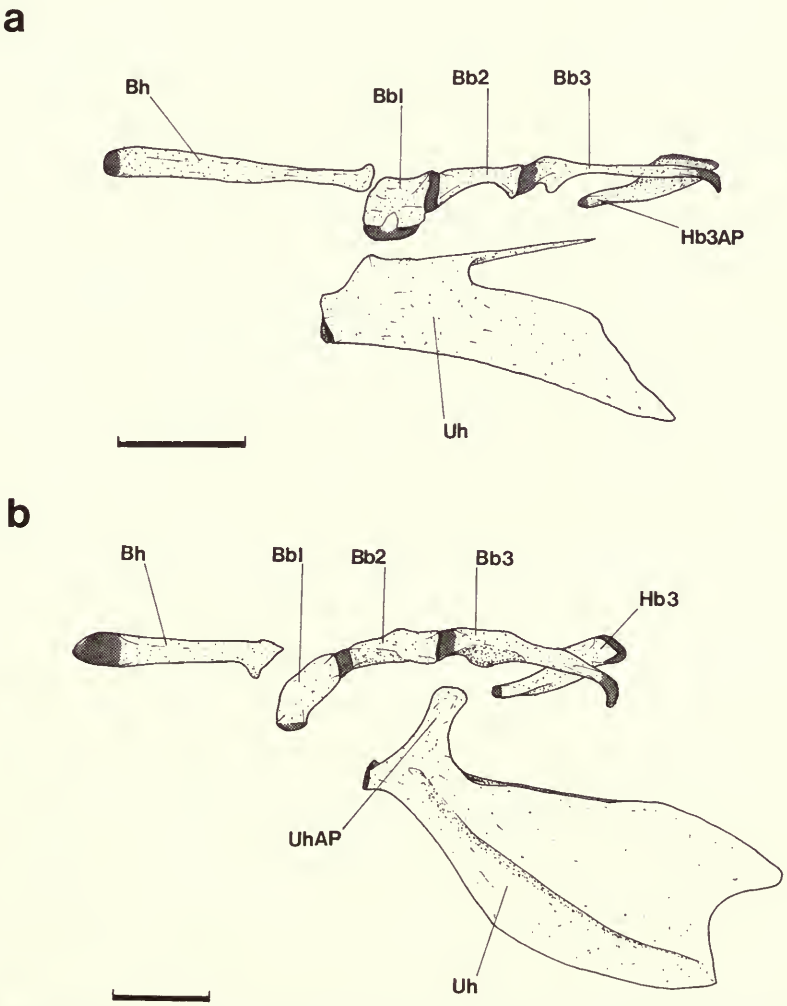

Fig. 16 Basibranchial/urohyal arrangement in: (a) *Lepomis macrochirus*; (b) *Scorpaenodes insularis*, lateral aspect, left side.

independently occurring in these taxa, and which has resulted in the complete loss of the keel.

The ventral edge of the keel on basibranchial 1 is cartilaginous in some mastacembeloids, and is correlated with the direct articulation of this bone with the urohyal. A faceted dorsal surface on the urohyal, or some form of ascending process generally articulating directly with basibranchial 1, is a characteristic feature of all Asian mastacembeloids apart from *Chaudhuria* which in this respect is similar to the African species (in all the urohyal lacks an ascending process or any form of articulation with basibranchial 1). A similar articulation is widespread among many perciform lineages and is particularly common among percoid families, (e.g. centropomids, percids, nandids, teraponids, cichlids, gadopsids and cepolids). The shape of the urohyal and its ascending process in these taxa is often specific to the family, as for example in the teraponids (Vari, 1978). In the centrarchids (e.g. *Lepomis macrochirus* Fig. 16a) the ventral edge of basibranchial 1 is cartilaginous, and articulates synchondrally with the urohyal in much the same manner as it does in some mastacembeloids (e.g. *Macrognathus* species). The scorpaeniforms also show a direct connection between the anterodorsal edge of the urohyal and basibranchial 1 (Fig. 16b).

The urohyal in beryciforms was found by Zehren (1979), to bear '. . . a short but distinct dorsally directed process for attachment of ligaments from the tips of the third hypobranchials'. I have found a similar arrangement of ligaments between hypobranchial 3 and the urohyal in the gadiforms (e.g. *Gadus morhua*) and ophidiforms (e.g. *Ophidion rochei* Fig. 17a), whereas the argentinoids (e.g. *Argentina silus* Fig. 17b) have the posterior end of their

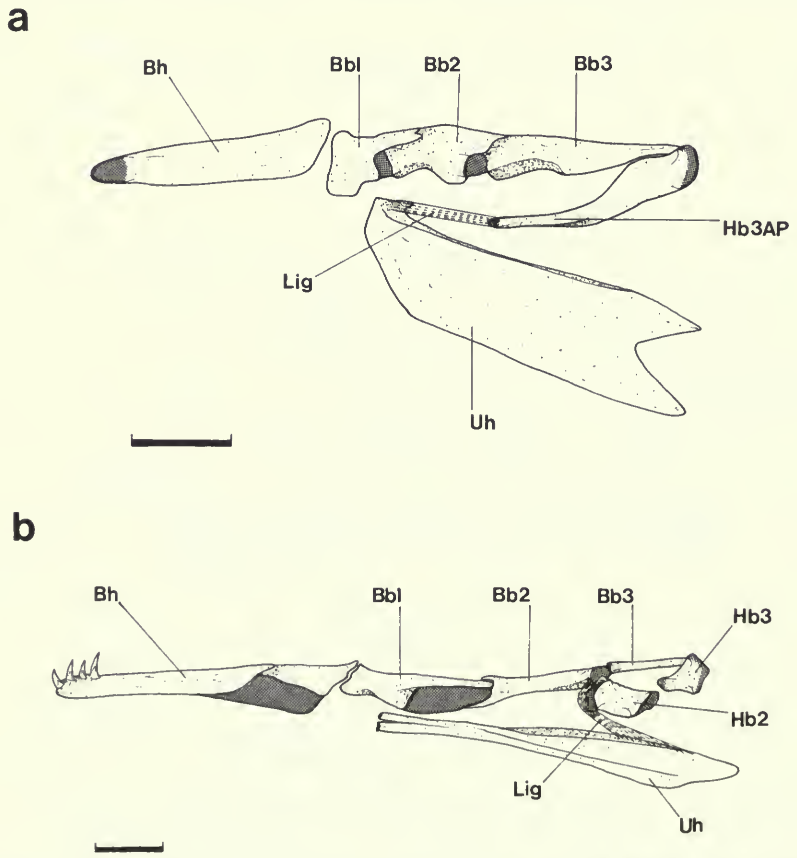

Fig. 17 Lateral view of the basibranchial/urohyal arrangement (left side) in: (a) *Ophidion rochei* (with ligamentous connection to hypobranchial 3); (b) *Argentina silus* (with ligamentous connection to hypobranchial 2).

long urohyal (which lacks an ascending process) ligamentously connected to the anterior tips of the second hypobranchials.

Among neoteleosts the development of an ascending process on the dorsal edge of the urohyal appears to be primitively associated with a ligamentous connection to the anterior tips of the third hypobranchials. During the course of neotelostean evolution these ligaments may have shifted their anterior connection from the urohyal to the basibranchials. Thus, the anterodorsal process on the urohyal, once freed from its ligamentous connection to the third hypobranchials, could become associated with the ventral surface of basibranchial 1. This developmental trend may result in the synchrondral articulation found between the keeled ventral edge of basibranchial 1 and the urohyal in various perciform taxa, including some mastacembeloids (e.g. *Macrognathus* species and *M. pancalus*) and such percoids as the centrarchids (e.g. *Lepomis macrochirus*).

An ascending process on the urohyal ventral to basibranchial 1 is widely distributed among many outgroups I have examined, as well as in most Oriental mastacembeloids, where it appears to be a retained plesiomorphy. This interpretation is consistent with the view expressed by Stiassny (1981: 98) that the urohyal ascending process is plesiomorphic in cichlids. Among Asian mastacembeloids the development of a direct articulation between the urohyal and basibranchial 1 is a derived condition, and is a synapomorphic feature of *Macrognathus* species and *Mastacembelus pancalus* (G–J in Fig. 19). This feature is another character indicating that *M. pancalus* is more closely related to *Macrognathus* species than to any other mastacembeloids.

The ascending process on the urohyal in *Mastacembelus sinensis* is connected to the ventral face of basibranchial 2 (Travers, 1984: fig. 52a) and is somewhat like the arrangement in *Mastacembelus zebrinus,* in which the long ascending process lies along the posterior edge of the keel on basibranchial 1 and has its tip connected to basibranchial 2 (Travers, 1984: fig. 52b). The unusual condition of the urohyal in these species appears to be autapomorhic for each. A low dorsal ridge on the urohyal in *Pillaia* (Travers, 1984: 46) lies below the ventral face of basibranchial 2 but a pair of ligaments from the anterior tips of the 3rd hypobranchials insert on the ridge's posterior edge, replicating the plesiomorphic condition.

The lack of an ascending process on the urohyal (or any form of direct articulation between it and basibranchial 1) is unique to *Chaudhuria* amongst the Asian taxa; most probably, having been secondarily lost it is an apomorphic feature that is convergent with the arrangement of the urohyal in the African mastacembeloids. For the African assemblage too, this character is a synapomorphy and may be cited as further evidence in support of their monophyletic origin.

The ventral processes on basibranchial 2 occur in two states that are of value in defining sublineages within the mastacembeloids. One of these states involves the anterior extension of the tip of the processes to a point where they form an arch over the first afferent branchial artery, and the connection by a short ligament, of each process to the posteroventral margin of the keel on basibranchial 1 (Travers, 1984: 92). Such arched processes are found only in some species of the assemblage which is also characterised by its members usually having fewer than 5 preopercular sensory canal pores (species complex L; see p. 118). In this assemblage the species with arched processes on basibranchial 2 are provisionally grouped into an unresolved polychotomy (termed L; see cladogram) because no characters have been found which can be used to resolve their interspecific relationships. In the second state basibranchial 2 lacks ventral processes. This is a condition found only in *Mastacembelus aviceps* (and possibly *M. latens), in Mastacembelus sinensis, Chaudhuria* and *Pillaia.* Although the condition of basibranchial 2 in these taxa resembles the plesiomorphic state, it is not necessarily a true plesiomorphy. *Mastacembelus aviceps* has been shown by numerous characters to be more closely related to the Zairean species *M. crassus* and *M. latens,* than to any other taxa. Similarly, *M. sinensis, Chaudhuria* and *Pillaia* appear to form a closely related group. Thus, the lack of ventral processes on basibranchial 2 in these taxa must be interpreted as a secondary, thus apomorphic loss which has occurred independently in both Asian and African groups.

Nelson (1969) first convincingly demonstrated a general evolutionary trend in teleostean gill arches towards the development of specialised structures by fusion and loss of dermal and endochondral elements.

The mastacembeloid gill arches lend support to his views, in particular the dorsal gill arch elements which have no uncinate process on the first or second epibranchial, lack a first and fourth pharyngobranchial (although the fourth toothplate is present), and have only a very small second pharyngobranchial with an equally small toothplate. This is the condition of the dorsal gill arches in most species.

The absence of fused toothplates on pharyngobranchial 2 is a further apomorphic development, and a synapomorphy for a group of African species comprising all those grouped in polychotomy L (on the basis of their arched basibranchial 2 ventral processes) and species M to S (see cladogram Fig. 19). The lack of a fused toothplate on pharyngobranchial 2 corroborates the evidence cited in support of the monophyletic origin of these taxa (see p. 119), and indicates the occurrence of a major dichotomy among African mastacembeloids.

The reductional trend involving pharyngobranchial 2 (i.e. the loss of its toothplate) culminates in the complete loss of the bone in one specimen of *Pillaia indica,* although in another specimen a well developed pharyngobranchial 2 is present. *Chaudhuria* and *Pillaia* both lack pharyngobranchial 2 toothplates, in this respect being convergent with the African taxa discussed above.

The ventral gill arch elements are also prone to reduction, by fusion or loss of dermal and endochondral elements. Such an apomorphic trend in the mastacembeloids involves the loss of an anterior process on hypobranchial 3 together with the loss of the ligaments connecting it to basibranchial 2.

A long anteroventral process on hypobranchial 3 typically occurs in most groups of higher euteleostean fishes. In some representatives of these groups there is what appears to be a loss of these processes, as shown for example in the synbranchids (Rosen & Greenwood, 1976: compare fig. 43 of ventral gill arch skeleton in *Ophisternon bengalense* with fig. 50 of the same elements in *Monopterus cuchia*). This situation is convergent with that in some mastacembeloids.

The lack of an anterior process on hypobranchial 3 is another synapomorphy uniting those mastacembeloids which have arched ventral processes on basibranchial 2 (p. 123), and provides further evidence in support of their monophyletic origin (i.e. complex L: Fig. 19).

If a fused toothplate on the dorsal surface of hypobranchial 3 is a synapomorphy of the mastacembeloids (p. 103) its absence in some taxa must be interpreted as a secondary loss. The fact that the toothplate is generally absent in those lineages characterised by reductional trends (e.g. *Pillaia* and *Mastacembelus paucispinis,* the undescribed *Mastacembelus, M. brachyrhinus, M. brichardi, M. aviceps* and *M. crassus*) lends weight to the view that its absence is a secondary loss.

The toothplate is also absent in five other species, namely *Mastacembelus mastacembelus, M. marmoratus, M. niger, M. sclateri* and *M. ubangensis,* the last four of which have been tentatively included in assemblage L. This assemblage is thought to be the sister group of species M to S (as they share the absence of a fused toothplate on pharyngobranchial 2, and have 4 or fewer preopercular sensory canal pores). The overlap in this character between some species in L and species M to S (for which it is a synapomorphy) serves to illustrate the point that further study may well reveal more complex interrelationships between these groups. The lack of a fused toothplate on hypobranchial 3 in *M. mastacembelus* (a species showing few reductional features) must presumably represent a further independent, secondary loss of this character convergent with that in *Pillaia* and the African species. However, in view of its rather mosaic distribution it is perhaps best not to rely too heavily on this character.

PECTORAL GIRDLE

The ability to burrow into the substrate is a phenomena independently acquired in a number of percomorph fishes, including the synbranchoids (Lüling, 1980), blennioids (Springer,

1968) and mastacembeloids. However, not all mastacembeloids burrow (Schofield, 1962) and in those that do (including *Mastacembelus zebrinus, M. pancalus* and the 3 *Macrognathus* species) this ability could be an underlying synapomorphy of the group. However, until more is known of the burrowing habits of all mastacembeloids, particularly the African taxa, a final decision cannot be made on its value as an indicator of phyletic relationships.

When burrowing, mastacembeloids employ a rapid side-to-side movement (pers. obs.) of a kind not described for any other burrowing species. This mechanism may account for the development of a large ventral limb of the cleithrum with a wide lateral face (presumably for extra muscle attachment) in *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species (Travers, 1984: 98). This feature is a synapomorphy of these taxa (species F to J in Fig. 19). In no other mastacembeloid taxon is a cleithrum of these proportions found.

Development of the cleithrum has been taken a stage further in *Mastacembelus zebrinus* (taxon F in cladogram). Here it has a particularly wide ventrolateral face protracted anteroposteriorly and connected with its opposite number medially to give the pectoral girdle a deep, 'keeled' appearance (Travers, 1984: fig. 67). This arrangement of the cleithrum is a species specific characteristic of *M. zebrinus.*

A reverse trend is seen in some species. The cleithrum is very slight in the highly derived species *Mastacembelus brichardi, M. aviceps* and *M. crassus* (and probably *M. latens*). This appears to be another evolutionary reduction associated with the small size of these micro- and cryptophthalmic species, and as such is treated as a synapomorphic character indicative of their shared recent common ancestry.

This trend is taken even further in the Tanganyikan *M. micropectus* which, as its name implies, has particularly small pectoral fins that may even be completely lacking from some individuals (pers. obs. and D. J. Stewart pers. comm.). *M. sinensis* and to a greater extent *Chaudhuria* and *Pillaia* also have small pectoral fins, but larger than those in the Zairean rapids species and *M. micropectus.*

The endemic species from the lower Zairean rapids and *Mastacembelus sinensis, Chaudhuria* and *Pillaia* from Asia, are characterised by numerous derived reductional features which have generally been treated severally as synapomorphies in this study. It could be argued that such an interpretation is incorrect on the grounds that they are inevitable consequences correlated with the small adult size reached by these taxa (i.e. paedo- or peramorphosis; Gould, 1977; Alberch, 1979; Fink, 1982). This, however, would be a gross oversimplification of the complex interaction of extrinsic (e.g. the highly specialised rapids environment) and intrinsic (e.g. genetic, hormonal or cellular) influences (morphogenetic processes) that appear to be moulding the morphology of these taxa which, anyhow, can in at least one species, have an adult size comparable to that reached by other mastacembeloids, from both Asia (e.g. *Mastacembelus maculatus*) and Africa (e.g. *Mastacembelus shiranus*), but which lack reductional features.

Primitively, the scapula is pierced by a large foramen in representatives from most major euteleostean lineages. In the more derived fishes, development of the foramen is known to follow various trends including its subdivision (e.g. in a number of beryciform families; Zehren, 1979), and its anterior migration. This migration results in the anterior border of the foramen becoming surrounded by the cartilage which lines the anterior edge of the scapula. A change in the position of the scapula foramen in this manner can be seen in a variety of perciform assemblages, including the mastacembeloids. The foramen lies across the anterior border of the bone and its cartilage surround in all African mastacembeloid taxa (Travers, 1984: 100), whereas, in all Oriental species, including *Mastacembelus sinensis, Chaudhuria* and *Pillaia*, the foramen is completely bone enclosed. Of these two conditions the former is the more derived and is a synapomorphy supporting the hypothesised monophyly of the African assemblage.

VERTEBRAL COLUMN

In all mastacembeloids, other than those with relatively low vertebral counts, an increase in the total number of vertebrae does not occur equally among abdominal and caudal elements; the number of caudal vertebrae is generally the greater by a count of 15–20.

With few exceptions, the African species have a proportionally larger number of caudal vertebrae when compared with the Asian lineages (Travers, 1984: 107). The increased number of caudal vertebrae in these African species is presumably an apomorphic development, and a further synapomorphy of this group.

If the several exceptional African species, which in contrast have a relatively low number of caudal (as opposed to abdominal) vertebrae, are arranged in order of their decreasing vertebral number, the sequence of species is much the same as that when the taxa are ranked according to their number of preopercular sensory canal pores (see p. 119), *viz., Mastacembelus paucispinis* (53 caudal vertebral); the undescribed *Mastacembelus* species (56); *Mastacembelus brachyrhinus* (45); *Mastacembelus crassus* (44); *Mastacembelus brichardi* (42) and *Mastacembelus aviceps* (38). The species having a count of caudal vertebrae below the modal number for African taxa (i.e. about 50) are all characterised by other reductional features.

Moderately small adult size and a deep body are features of all burrowing species (including polychotomy E, and species F to J). These taxa have very elongate, narrow neural and haemal spines compared with those in other species. The relatively long, narrow neural and haemal spines are a synapomorphy of the species complex E, F to J. The moderately small body size in these fishes, relative to that in the majority of mastacembeloids, may be correlated with low vertebral number, and possibly with burrowing habits. An average total count of less than 70 vertebrae was not found in any other mastacembeloids apart from those showing even greater overall reduction in adult size. Thus, in these species (i.e. complex E and F to J) a low vertebral count is treated as a further synapomorphy.

Epicentral and epipleural ribs are a common feature in all mastacembeloids, and are generally present on the 1st to 6th abdominal vertebrae (Travers, 1984: 107). *Mastacembelus sinensis, Chaudhuria* and *Pillaia* are exceptional in that they lack epipleural ribs and have 3 or less epicentral ribs. This low number, relative to the number in all other species is another reductional feature characterising these taxa. Representatives of other perciform assemblages generally have epipleural ribs, the plesiomorphic number being from 4–6. In this respect the majority of mastacembeloids retain the primitive condition, and the absence in *M. sinensis, Chaudhuria* and *Pillaia* is a synapomorphy for these taxa.

Pleural ribs are generally present on all but the first 4 or 5 abdominal vertebrae (Travers, 1984: 107) in mastacembeloids. In some species, including *Mastacembelus brachyrhinus, M. brichardi,* possibly *M. latens, M. crassus* and *M. aviceps* (species O–S in cladogram; Fig. 19) the ribs are confined to the posterior abdominal vertebrae and may only appear on the 20th and subsequent abdominal vertebrae (Travers, 1984: 109). In other eel-like neoteleosts with high abdominal and caudal vertebral numbers, pleural ribs generally appear by the 3rd or 4th abdominal vertebrae. This is the case in the percoid *Cepola rubescens,* the blennioid *Pholidichthys leucotaenia* and the ammodytoid, *Ammodytes tobianus*. Pleural ribs apparently occur on all abdominal vertebrae in synbranchids, but in the congrogadids (e.g. *Congrogadus subduceus*) they are present on only the first 6 abdominal vertebrae. The presence of pleural ribs on the anterior vertebrae appears to be a plesiomorphic condition among percomorph fishes.

The absence, in some mastacembeloids, of pleural ribs from more than the first 4 or 5 abdominal vertebrae is, therefore, an apomorphic condition. The lack of pleural ribs on the first 12 to 20 abdominal vertebrae is a synapomorphic character for *Mastacembelus brachyrhinus, M. brichardi, M. crassus,* and *M. aviceps* (and probably *M. latens*). Five species endemic to Lake Tanganyika also lack pleural ribs on the first 11 to 16 vertebrae. These species are: *Mastacembelus albomaculatus, M. moorii, M. ophidium, M. tanganicae* and *M. micropectus.* Unfortunately, no further characters were found that unite this group or any of its constituent species with the other taxa showing this derived character and the resemblance must be treated as a case of convergence.

Dorsal and anal fin spines

Although the number of dorsal spines varies both inter- and intraspecifically, two groups of species (the *Macrognathus* species, and *Mastacembelus paucispinis* and its undescribed close relative) are distinguished by their comparatively low number of spines.

The low spine numbers in these species have been effected in different ways (see Travers, 1984: 110). In the *Macrognathus* species, the spines are lost from the anterior part of the series but in *Mastacembelus paucispinis* and the new *Mastacembelus* species the spines are lost from the posterior part of the series. The loss of anterior spines is a synapomorphy of the *Macrognathus* species, whilst the posterior loss of spines (associated with an increase in length of the soft-rayed dorsal fin) is a synapomorphy for *Mastacembelus paucispinis* and the undescribed *Mastacembelus* species. The actual number of dorsal spines in *Mastacembelus paucispinis* (7–10) is the lowest found in any spined mastacembeloid examined and is peculiar to this species as are the 15 or 16 found in all specimens of the undescribed species (T. Roberts pers. comm.).

Three anal spines occur in many acanthopterygian fishes (Patterson, 1964; Zehren, 1979). The first 2 are often supported by a single massive pterygiophore connected proximally with the haemal 'cross-bar' of the first caudal vertebra. The third spine is often smaller than the second and may be hidden within a deep skin fold. This arrangement of the anal spines occurs in most perciform assemblages, including the mastacembeloids and is considered to be the plesiomorphic condition.

Among the mastacembeloids there are two exceptions to this arrangement. In *Mastacembelus sinensis* the third anal spine is separated by a distance of 4 vertebrae from the second spine which it equals in size (Travers, 1984: fig. 74), and represents an autapomorphic character of the species. The second exceptional arrangement is the absence of both anal and dorsal spines in *Chaudhuria* and *Pillaia* (Travers, 1984: 109). The absence of fin spines in percomorph fishes is rare (a condition seen for example in some highly aberrant forms such as the schindleroids), and the presence of both anal and dorsal spines among all other mastacembeloids (and the vast majority of percomorph taxa) lends support to the view that the absence of spines in *Chaudhuria* and *Pillaia* must be a character loss associated with the reductional trends manifest in many features of their anatomy.

Intermediate between this condition and the usual one is the presence of two anal spines (supported by a single pterygiophore) in several West African species (e.g. *Mastacembelus batesii, M. brevicauda, M. flavomarginatus, M. greshoffi, M. loennbergii, M. nigromarginatus* and *M. reticulatus*) and two from the Zairean rapids fauna (e.g. *Mastacembelus aviceps* and *M. crassus*). This apomorphic feature may have developed independently or be a synapomorphy for the group. A single anal spine is unique to *M. ophidium* and is an autapomorphic character.

Caudal fin

The arrangement of the caudal skeleton in euteleostean fishes has been summarised by Rosen (1973). Although there is no synapomorphic character uniquely confined to the caudal skeleton of all mastacembeloids, there are significant reductional features which may be used to distinguish major lineages within the group.

The large assemblage recognised as the sister-group to *Mastacembelus sinensis, Chaudhuria* and *Pillaia* can be divided into two groups on the basis of caudal anatomy, namely taxa from SE. Asia and the Middle East (Oriental mastacembeloids), and those from Africa.

Almost all the Asian mastacembeloids (including the Middle Eastern form) have only four hypural elements, an apomorphic condition compared with the six hypurals usual in euteleosteans (Rosen, 1973). The two elements lying below the mid-lateral axis of the vertebral column represent the 1st and 2nd hypurals whilst two dorsal plates represent the upper hypural elements. Faint sutures can often be seen in the upper plates and seem to indicate that they have originated during ontogeny by fusion of separate hypurals present at an early stage of morphogenesis.

Among the Asian (and Middle Eastern) species which otherwise have 4 hypural plates, one species, *Macrognathus aculeatus,* has five elements. As this species is united to other members of this group by a complex of synapomorphic characters (discussed below p. 135) the presence of an extra hypural must be interpreted as the retention of the plesiomorphic condition.

Mastacembelus pancalus (Travers, 1984: fig. 75a) is another exception as it has only a single upper and a single lower hypural plate. This highly derived condition of the hypurals is convergent with that found in some African species (see below).

The presence of 4 hypurals is a synapomorphy of those Asian and Middle Eastern species recognised in the cladogram as two unresolved polychotomies (D & E) and the species complex F to J, this character is evidence in support of the monophyletic origin of this assemblage. The apomorphic hypural number in these mastacembeloids is associated with a number of plesiomorphic caudal characters. These include a relatively high number of principal caudal fin rays (generally 16–18, although there are only 12 in *Mastacembelus pancalus,* and as many as 20 to 21 in *M. keithi* and *M. albomaculatus*); a relatively high number of epurals (e.g. 3 in *Mastacembelus pancalus,* although there are only 2 in *M. unicolor, M. maculatus* and *M. erythrotaenia*); and a distinct caudal fin in several species (although the fin is confluent basally with the dorsal and anal in *Mastacembelus erythrotaenia, M. maculatus, M. caudiocellatus* and *M. circumcinctus*).

All the African taxa show a further development of the trend towards reduction in the caudal skeleton through loss or fusion of hypural elements.

The taxa comprising this group are represented in the cladogram by unresolved polychotomy L, the complex of species K, and species M to S. They are united by a general occurrence in the caudal skeleton of only 2 (occasionally 3, sometimes 1) hypural bones. The 4 hypurals found in a single specimen of *Mastacembelus vanderwaali* are exceptional; an examination of 5 further specimens revealed only 2 separate hypurals to be present in all (Travers, 1984: fig. 76a).

When a total of more than 2 hypural plates is present in species of this group, the additional elements are invariably in the upper part of the fin skeleton, the lower element always remaining a single plate. Two upper hypural plates are present in *Mastacembelus moorii, M. ophidium*, *M. paucispinis* and the undescribed species and, 3 in the one specimen of *M. vanderwaali.* This arrangement in *M. vanderwaali* differs from that in the Asian species whose hypural complement is made up of two upper and two lower elements.

The trend towards hypural fusion among the African species reaches its climax (probably independently) in *Mastacembelus aviceps, M. ellipsifer,* and possibly also in *M. flavidus* and *M. brachyrhinus* (see below). In these species there is a single large hypural plate although its posterior edge is indented slightly in the mid-lateral axis in *M. ellipsifer* and *M. aviceps*, and a faint suture can be detected running from a similar indentation to the base of the hypural plate in *M. flavidus* and *M. brachyrhinus.*

The presence of 2 hypurals (or even a single plate) is a synapomorphy of the African mastacembeloid species, which together with their high numbers of caudal vertebrae, incompletely enclosed scapula foramen, and lack of a urohyal ascending process, is evidence in support of the monophyly of this assemblage. The hypural arrangement in this group is associated with a number of other apomorphic caudal features. These include, a tendency for there to be less than 10 principal caudal fin rays (there are only 4 in some cases e.g. *M. zebratus*), a fused, short, spatulate and non-ray supporting haemal spine on the 2nd preural vertebra, and for the caudal fin to be confluent with the dorsal and anal fins.

The assemblage of Asian species comprising *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (taxa A to C) is recognised as the sister group of all other mastacembeloid assemblages combined (see p. 132). The caudal skeleton in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* is composed of two hypurals (an upper and lower element), a single epural (a uroneural could not be distinguished), the second preural centrum with fused neural and haemal arches that support short spines, confluence of the caudal with the dorsal and anal fins (apart from in *Chaudhuria*, Travers, 1984: 43) and only 8 to 10 principal caudal fin rays. The caudal fin skeleton in this group superficially resembles that in the African taxa since they share the general occurrence of only 2 hypurals, the lack or at most only a single epural, and have neural and haemal arches (with short spines) fused to the 2nd preural vertebra. The African taxa, however, are united by three synapomorphies (the lack of an ascending process on the urohyal or a direct articulation between it and basibranchial I, the scapular foramen not completely bone enclosed, and the tendency for there to be a high ratio of caudal to abdominal vertebrae) which are not found in *M. sinensis, Chaudhuria* or *Pillaia*. Furthermore, all other Oriental mastacembeloids share a synapomorphy (hyomandibula/metapterygoid separation) with the African taxa that is not found in *M. sinensis, Chaudhuria* and *Pillaia*. Thus, the African mastacembeloids share a more recent common ancestry with the larger group of Oriental taxa and because of the numerous synapomorphies shared by *M. sinensis, Chaudhuria* and *Pillaia* (see p. 132 for summary), the caudal fin resemblances between these taxa and the African species are thought to have been independently evolved.

This convergence is most clearly seen in those African species from the lower Zairean rapids (e.g. *M. brachyrhinus, M. brichardi,* possibly *M. latens, M. crassus* and *M. aviceps*; O–S in Fig. 19) and is repeated in several other characters (including features of the orbital and otic regions of the neurocranium p. 110 & 111; the upper jaw p. 113; the ectopterygoid p. 118, and the ventral gill arches p. 121).

SQUAMATION

The mastacembeloids are typically covered in small scales which generally extend over the entire body apart from certain regions of the head. In *Mastacembelus latens* (Roberts & Stewart, 1976), *M. crassus* and *M. aviceps* scales are absent. A total lack of scales is not found in any other taxa apart from *Chaudhuria* and *Pillaia* (Travers, 1984: 115). The loss of scales is but one of many reductional characters found in these taxa. For the reasons discussed above, the nakedness of these African and Asian taxa is considered to have evolved independently and can be added to the list of reductional features occurring convergently in *Chaudhuria, Pillaia,* and species from the lower Zairean fauna.

The presence of scales on only the posterior third of the body in *Mastacembelus micropectus* is a further autapomorphy for this species (see p. 125).

Myology

CEPHALIC MUSCLES

The maxillo-mandibular ligament occurs in most mastacembeloids except several Asian taxa (including *Mastacembelus zebrinus, M. pancalus,* the *Macrognathus* species, and *Mastacembelus sinensis*).

The widespread occurrence of this ligament throughout the teleosts (Winterbottom, 1974) suggests that its loss is an apomorphic reductional feature. It is, therfore a further synapomorphy uniting *Mastacembelus zebrinus, M. pancalus* and *Macrognathus,* which in the absence of any further characters must be considered to have occurred independently (as reductional characters are inclined to do, see p. 110) in *Mastacembelus sinensis.*

A differential development of parts of the *adductor mandibulae* is a myological feature associated with the large rostrum in some mastacembeloids. Part A_2 is generally the dominant part of the adductor complex in teleosts, and the majority of mastacembeloids are no exception. However, in those species with a large rostral appendage part A_1 is greatly enlarged and is the dominant part of the complex (e.g. *Mastacembelus caudiocellatus, M. circumcinctus M. keithi, M. maculatus, M. guentheri* and possibly *M. perakensis* [for which material was unavailable] i.e. polychotomy E, and in *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species i.e. F to J in the cladogram). The hypertrophy of part A_1 is probably correlated with its involvement in the movement of the rostral appendage (see Gosline, 1983: 325). However, the mechanism described by Gosline (*op. cit.*) overlooks several other features (discussed below) which also directly control movement of the rostrum.

The tendency for part A_1 to develop as the largest part of the adductor complex is a synapomorphic character of the mastacembeloid group comprising polychotomy E and species F to J.

In *Mastacembelus brachyrhinus, M. brichardi, M. aviceps, M. crassus,* and possibly *M. latens* (i.e. species O–S) the superficial adductor mandibulae musculature (Part A_1 & A_2) has hypertrophied to such an extent that these species are clearly distinguishable from all others. Part A_2 is particularly large and has expanded its site of origin dorsally across the dorsolateral wall and roof of the neurocranium (Travers, 1984: 125). A morphocline involving the extent to which A_2 overlies the dorsal surface of the neurocranium is clearly seen in these species (i.e. O to S). The hypertrophy of part A_2 is a synapomorphy uniting *M. brachyrhinus, M. brichardi, M. crassus* and *M. aviceps* (and probably *M. latens*) and may be related to the reduced eye size in these species, allowing the muscle to expand into the orbit; an arrangement also found in the synbranchids and several microphthalmic catfishes (P. H. Greenwood, pers. comm.). A similar, although less extreme development of the *adductor mandibulae* $A_{1\&2}$ also occurs in two Lake Tanganyikan species (*Mastacembelus albomaculatus* and *Mastacembelus micropectus*) and in *Pillaia,* species which are also characterised by their relatively small eyes.

The *adductor arcus palatini* lies between the ventrolateral wall of the neurocranium and the hyopalatine arch in all mastacembeloids (Travers, 1984: 120); its anterior fibres form the orbital floor. In this form the *adductor arcus palatini* is a characteristic of more advanced teleosts (Winterbottom, 1974: 238). In some taxa e.g. *Mastacembelus caudiocellatus, M. circumcinctus, M. guentheri, M. keithi, M. maculatus* and *M. perakensis* (i.e. all species provisionally placed in the unresolved polychotomy E), and in *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species (i.e. species F–J), the anterior fibres extend from the anterolateral face of the parasphenoid across the anterior surface of the ectopterygoid and insert along the attenuated posterior edge of the large first infraorbital bone. This anterior enlargement of the *adductor arcus palatini,* like hypertrophy of A_2, is a synapomorphy of species group E and species F to J.

The enlargement of the anterior region of the *adductor arcus palatini* (like the hypertrophy of the *adductor mandibulae* A_2) is associated with the large rostral appendage in members of taxa E to J. A clear morphocline in the development can be distinguished, beginning with the few fibres that insert on the first infraorbital in *M. keithi* and *M. zebrinus* (Travers, 1984: fig. 88a) and terminating in the broad muscle block virtually separated off from the anterior end of the adductor in *Macrognathus aculeatus* (Travers, 1984: fig. 88b).

The size and degree of independence of the anterior region of the *adductor arcus palatini* is directly correlated with the size of the rostral appendage. The greatest hypertrophy, and the greatest degree of its independence from the main muscle mass, occurs in species with the largest rostral appendage and highest number of rostral toothplates; *M. aculeatus.* Correlated with these changes in the *adductor arcus palatini* is the extent to which the posterior edge of the 1st infraorbital bone is attenuated posterodorsally (Travers, 1984: compare fig. 79b with fig. 86 a, b & c).

Other features of that warrant attention include:
Variation in the form of the rim around the anterior nostril.

The mastacembeloids have both an anterior and a posterior opening to the hypertrophied olfactory sac (p. 107). The posterior nostril is covered by a small flap of skin that can be moved voluntarily in order to open or close it. The anterior nostril lacks a distinct cover, although a number of skin folds lie around the rim. In the majority of species these folds are generally composed of two larger flaps (fimbrules) between which are two narrower ones (fimbriae; see fig. 13a). These flap-like skin folds apparently are used to prevent particles of substrate or debris from entering the anterior nasal opening (Roberts, 1980). In some species the two fimbrules appear to be subdivided, resulting in 6 narrow digitform fimbriae around the rim of the anterior nostril (Fig. 13b). This condition was originally described by Roberts (*op. cit.*) in several Asian mastacembeloids. I have found it (in association with the presence of a relatively large rostral appendage i.e. the apomorphic condition) to occur in *Mastacembelus caudiocellatus, M. circumcinctus, M. guentheri, M. keithi, M. maculatus* and probably *M. perakensis* (species comprising polychotomy E) and *Mastacembelus zebrinus,* *M. pancalus* and the *Macrognathus* species (species F to J in cladogram), and to be a synapomorphy of these taxa. Such an interpretation supports the view originally expressed by Roberts (1980: 390) that, 'This morphological dichotomy ultimately may . . . indicate the derivation of *Macrognathus* from a group of species within *Mastacembelus* that is largely or entirely restricted to Asia'.

II. Intrarelationships of the Mastacembeloidei

The currently recognised intrarelationships of the mastacembeloids as expressed in the present classification of the group (summarised in Fig. 18) cannot be retained since most of the categories are demonstrably non-monophyletic.

Numerous shared derived characters linking taxa at various hierarchical levels strongly suggests that the present delimitation of families and genera is 'unnatural', the result of species being united or separated mainly by the supposed magnitude of their morphological differences and without any attempt to unravel genealogical relationships. For example, at one extreme this practice has resulted in *Pillaia* (and *Garo* see p. 109) being placed in a separate family (Pillaiidae) mainly because of their single upper jaw element, whilst at the other extreme it has resulted in numerous species being lumped in a single genus.

A revision of the intrarelationships of the mastacembeloids based on 77 principle synapomorphies and 27 autapomorphies (several of which occur convergently in some taxa), is outlined in a cladogram (Fig. 19). The cladogram is arranged around 17 nodal points, each of which represents a character or set of characters found in those taxa above the node.

The first node represents a character complex of 18 synapomorphies which are derived features defining the Mastacembeloidei (discussed above p. 108).

The second node represents 10 derived characters (nos. 25–34) and defines one of the two major sister groups into which the mastacembeloids can be divided.

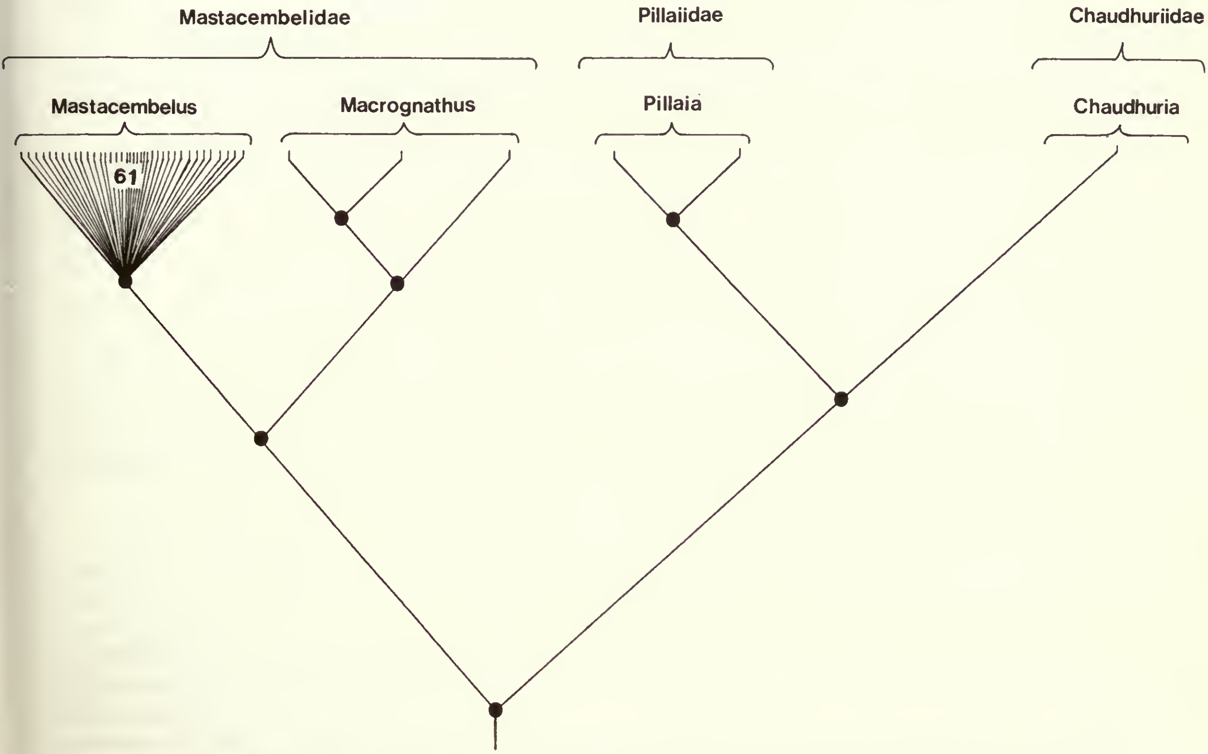

Fig. 18 Relationships of mastacembeloid taxa, as shown by the classification in current use.

These synapomorphies may be summarised as follows:

25. Long narrow posterior parasphenoid processes (p. 111).
26. Dorsomedial processes of the exoccipitals separated by the supraoccipital (p. 112).
27. Dorsal surface of the exoccipital perforated (p. 112).
28. 1–2 inner rows of premaxillary teeth (p. 113).
29. Loss of endopterygoid (p. 116).
30. Ectopterygoid with narrow lateral face (p. 118) and very long anterodorsal process.
31. Palatine reduced in size (p. 118).
32. Interdigitating processes of anterior and posterior ceratohyals reduced or lost (p. 119).
33. Loss of ventral processes on basibranchial 2 (p. 123).
34. Loss of epipleural ribs and 3 or less epicentral ribs (p. 126).

On the basis of these synapomorphies *Mastacembelus sinensis* (species A) is united with *Pillaia* (B, i.e. *P. indica* and presumably *Garo khajuriai* although no material was available for dissection of this species) and *Chaudhuria* (species C, i.e. *C. caudata*) in an assemblage that forms the sister group to all other mastacembeloids.

Although 6 (28, 29, 31, 32, 33 & 34) of the 10 characters defining this lineage are reductional or loss characters that could have arisen independently within the mastacembeloids, they are always found in association with the other 4 characters (25, 26, 27 & 30) that define the taxon. In combination these characters are considered to be reasonable indicators of recent shared common ancestry.

Chaudhuria and *Pillaia* (incorporating *Garo*) share more apomorphic characters than either does with *Mastacembelus sinensis.* The latter species may be defined on the basis of 2 autapomorphies *viz:*

35. Long urohyal dorsal process ascends vertically and tip contacts underside of basibranchial 2 (p. 123).
36. Large 3rd anal spine, equal in size to the 2nd, and separated from it by a distance of 4 vertebrae (p. 127).

The 3rd node in the cladogram represents 14 derived features that link *Chaudhuria* (C) and *Pillaia* (B inclusive of *Garo*) more closely to one another than to any other mastacembeloid. These synapomorphies are:

37. Posterior end of vomerine shaft ventrally depressed (see Travers, 1984: 43 & fig. 15ai & bi).
38. Loss of pterosphenoid (p. 110).
39. Loss of basisphenoid (p. 110).
40. Single foramen in pars jugularis (p. 111).
41. Large saccular bulla lying within the prootic, exoccipital and basioccipital (p. 112).
42. Loss of frontal descending lamina (p. 113).
43. Cephalic sensory canal system reduced or lost (p. 113).
44. Cornomeckelian a small ossicle on medial face of anguloarticular (p. 115).
45. Loss of palatine (p. 116).
46. Ectopterygoid articulation with lateral ethmoid absent, its long anterodorsal arm contacting the vomerine shaft (p. 116).
47. Loss of pharyngobranchial 2 toothplate (p. 124).
48. Loss of dorsal and anal spines (p. 127).
49. Scaleless (p. 129).
50. Extremely small adult size (see Travers, 1984: 32 & 43).

Apart from characters 37 and 46 all these characters are reductional ones (i.e. losses or presumed secondary redevelopments of the plesiomorphic condition). As such they could have arisen independently in more than one lineage. In fact, this is the case with three (39, 40 and 49) which are also found in the highly aberrant African taxa *Mastacembelus crassus* and *Mastacembelus aviceps* (and possibly *M. latens*; taxa Q to S in the cladogram). However, characters of this type are not excluded (see p. 110) and are used because of their congruence with each other as well as with a uniquely derived character (37). This problem is frequently encountered in the analysis of phylogenetic relationships. It is common among systematic studies of perciform lineages (especially the more generalised basal percoids) and has recently been discussed by Johnson (1980: 42) who observed: '. . . the sharing of a number of reductive specialisations in identical states is a reasonable indicator of affinity, even if each character cannot be shown to be uniquely derived'. The problem has also recently been highlighted in characiform studies by Weitzman & Fink (1983: 345). These authors agree with Johnson (*op. cit.*), but draw attention to the need for comparisons between developmental stages in taxa under the influence of what appear to be heterochronic ontogenetic changes, with similar stages in appropriate outgroups.

Three of the characters used to unite *Chaudhuria* and *Pillaia* (41, 44 & 48) would, at least superficially, appear to be the plesiomorphic condition of the feature. In this instance however, the characters are thought to be secondary redevelopments of the plesiomorphic condition (i.e. plesiomorphic mimics) because this is the most parsimonious explanation in view of the many apomorphic characters shared by *Chaudhuria* and *Pillaia* and all other mastacembeloid taxa (see defining characters, p. 108).

Chaudhuria caudata (C) may be defined on the basis of the following 3 apomorphic characters not found in any other mastacembeloids:

51. Ventral edge of dentary divided (p. 114).
52. Dorsal and anal pterygiophores and fin rays absent from the last 6 or 7 caudal vertebrae, associated with a distinct caudal fin (see Travers, 1984: 43 & fig. 23a).
53. Loss of rostral appendage (p.108).

Pillaia indica (B) may be defined on the basis of 4 apomorphies:

54. Loss of prootic anterior process and fused toothplate on hypobranchial 3 (p. 111 & 124).
55. Single upper jaw element (p. 113).
56. Paired neural spines on many abdominal vertebrae, with a wide opening in the dorsolateral face of the neural arch in most caudal vertebrae (see Travers, 1984: 48 & fig. 22).
57. Microphthalmic (p. 111 & 130).

Most of these characters are reductions and losses that could have arisen independently in several of the highly derived African taxa (e.g. species P to S, discussed below).

The 4th node in the cladogram represents a synapomorphy defining the second major group in the basic mastacembeloid dichotomy, *viz:*

58. Hyomandibula and metapterygoid widely separate, and associated with a large symplectic (p. 116).

This feature unites the majority of mastacembeloid taxa (D to S in the cladogram Fig. 19).

The assemblage may be divided into two principal subgroups as indicated by the 5th and 11th nodes in the cladogram.

The 5th node represents a single synapomorphy:

59. 4 separate and autogenous hypurals (p. 127).

This feature defines a group comprising all the Oriental mastacembeloids (D to J in cladogram) except *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (see above), and which forms the sister group to the African mastacembeloids (taxa K to S, united by node 11 in the cladogram).

Two major sublineages are recognised within the species group D to J.

The first sublineage (D) comprises 6 of the 15 Oriental species recognised by Sufi (1956), and is defined by a single synapomorphy, *viz:*

60. Anterior arm of endopterygoid long and lies between the ectopterygoid and lateral ethmoid connection (p. 116).

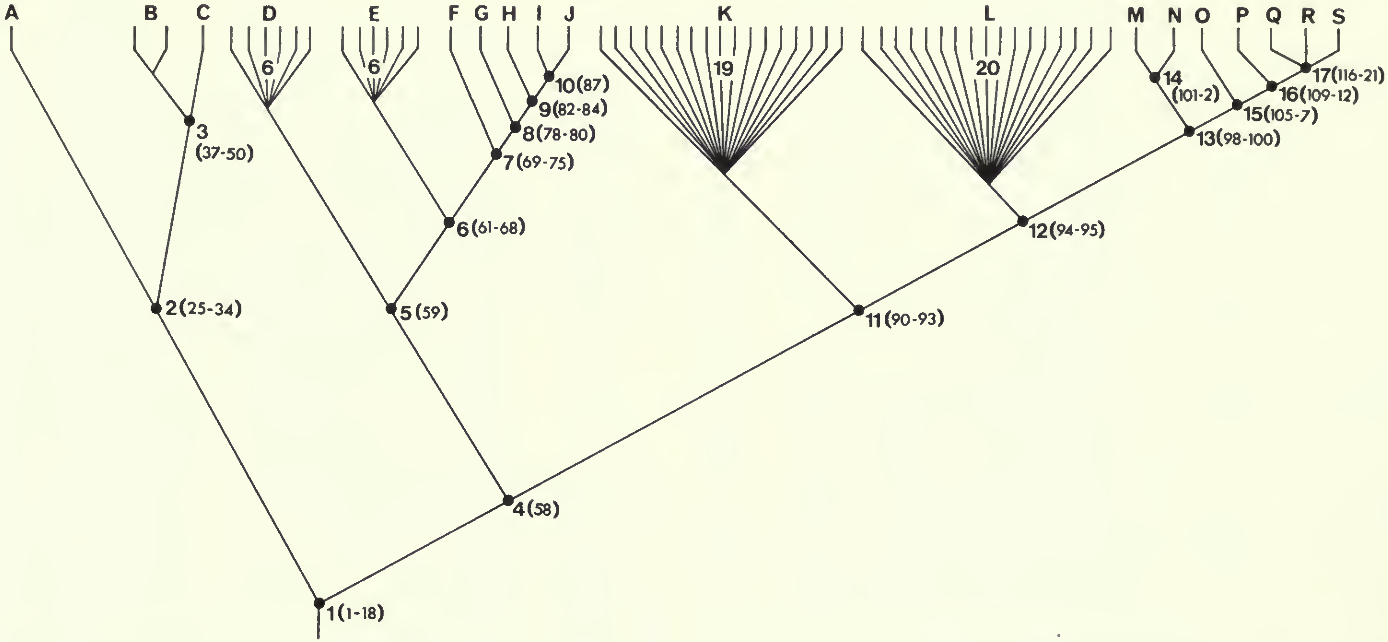

Fig. 19 Cladogram illustrating the proposed phylogenetic intrarelationships of the Mastacembeloidei. Scheme composed of 17 nodes based on principal synapomorphies (given in brackets) listed in text, and autapomorphies and derived characters defining, respectively, individual species (A,C,F,G,H,I,J,M,N,O,P,Q,R and S) and species groups (B,D,E,K, and L). *Key to species and species groups:* A *Mastacembelus sinensis*; B *Pillaia indica* and *Garo khajuriai*; C *Chaudhuria caudata*; D Assemblage of six species (listed on p. 135); E Assemblage of six species (listed on p. 135); F *Mastacembelus zebrinus*; G. *Mastacembelus pancalus*; H *Macrognathus aculeatus*; I *Macrognathus aral*; J *Macrognathus siamensis*; K Unresolved polychotomy (species included listed on p. 137); L Unresolved polychotomy (species included listed on p. 137); M *Mastacembelus paucispinis*; N Undescribed *Mastacembelus* species (Roberts & Travers, in prep); O *Mastacembelus brachyrhinus*; P *Mastacembelus brichardi*; Q *Mastacembelus latens* (provisional, pending further specimens); R *Mastacembelus crassus*; S *Mastacembelus aviceps*.

This character is present in *Mastacembelus armatus, M. erythrotaenia, M. mastacembelus, M. oatesii* and *M. unicolor. Mastacembelus alboguttatus* is tentatively assigned to this group because of its superficial resemblance to the other members, but lack of material precludes a definite decision on its membership.

No other characters were found that make it possible to analyse further the interrelationships of these 6 species which, therefore, are treated as an unresolved polychotomy (D). If polychotomies of this type prove to be inherently unresolvable they could reflect an evolutionary reality (Eldredge & Crancraft, 1980).

The other sublineage stemming from the 5th node (E to J) is defined by 8 synapomorphies, represented by the 6th node in the cladogram, *viz:*

61. Posterior region of parasphenoid undivided, apart from its tip, and excavated to form a pit-like depression on ventral surface (p. 111).
62. Expanded ventrolateral face of exoccipital and posteroventral margin of basioccipital, associated with deep basicranium (p. 111).
63. Deep basioccipital fossa accommodates anterior end of Baudelot's ligament (p.111).
64. Dorsal surface of frontal slopes ventrolaterally (p. 113).
65. Elongate narrow neural and haemal spines, associated with a deep body (p. 126).
66. Relatively low total vertebral count (see p. 126 & Travers, 1984: table 5).
67. Distinct anterior part of *adductor arcus palatini* muscle inserts on the attenuated posterior edge of the 1st infraorbital (p. 130).
68. 6 slender, digitiform fimbriae around rim of each anterior nostril, associated with relatively long rostral appendage (p. 130).

This sublineage contains the remaining 8 *Mastacembelus* species recognised by Sufi (1956) and the 3 *Macrognathus* species recognised by Roberts (1980). It represents a monophyletic assemblage defined by at least 3 unique synapomorphies (61, 67 & 68). Apart from the characters visible without dissection (e.g. 64 & 68), and those visible in radiographs (e.g. 65 & 66), the remaining characters could not be checked in every species because suitable material for dissection was not always available. For that reason *Mastacembelus guentheri, M. keithi* and *M. perakensis* have been placed with *Mastacembelus circumcinctus, M. caudiocellatus* and *M. maculatus* in an unresolved polychotomy (E) pending further research. Detailed studies of *Mastacembelus zebrinus, Mastacembelus pancalus, Macrognathus aculeatus, Macrognathus aral* and *Macrognathus siamensis* however, have revealed a nested series of synapomorphic characters which clearly show the phylogenetic affinity of these species (F to J). The 7th node represents the 7 synapomorphies shared by species F to J, *viz:*

69. Anterolateral expansion of premaxillary tooth-bearing alveolar surface (p. 113).
70. Low and broad coronoid process on dentary associated with tendency for its medial face to the toothed (p. 114).
71. Dorsal edge of anguloarticular with low, broad-based coronoid expansion (p. 115).
72. Indented anterolateral edge of quadrate (p. 116).
73. Tendency for ventral limb of cleithrum to develop a wide lateral face (p. 125).
74. Loss of the maxillo-mandibular ligament (p. 129).
75. Tendency for A_1 to become the largest part of the *adductor mandibulae* muscle, and for tA_1 to be a long, strap-like tendon extending to rostral appendage (p.129).

This suite of characters could be considered as a single transformation as they appear to be closely correlated (i.e. all can be functionally associated with the jaw mechanism) and may result from a common heterochronic ontogenetic shift. *Mastacembelus zebrinus* (species F) shows the suite of synapomorphies represented by the 7th node in the cladogram and is defined by two autapomorphies:

76. Extremely wide ventrolateral face of cleithrum producing 'keeled' pectoral girdle (p. 125).
77. Urohyal ascending process long and thin, its dorsal tip contacting basibranchial 2 and anterior margin connected to the posterior edge of the keel on basibranchial 1 (p. 123).

The 8th node represents 3 synapomorphies that unite *Mastacembelus pancalus* (species G) more closely with the *Macrognathus* species than to any other mastacembeloid.

These characters are:

78. Loss of palatine spur (p. 118).
79. Preopercular sensory canal with 3 central pores at the end of short descending branches (p. 119).
80. Basibranchial 1 keel with a cartilaginous ventral edge and direct articulation with the urohyal (p. 122).

Although characters 79 and 80 are both neomorphs, character 78 is a reductional one and as such could have arisen independently (see p. 118) as it does in *Mastacembelus maculatus*. However, in combination with the two other apomorphic characters it is considered to be a reliable indicator of the close phylogenetic relationship between these species.

Mastacembelus pancalus is defined by a single autapomorphy:

81. Faceted connection between anteromedial margin of quadrate and posterolateral face of ectopterygoid (p. 118).

The 9th node in the cladogram represents 3 synapomorphies that unite the *Macrognathus* species (H to J). These can be summarised as follows:

82. Fragmentation of premaxillary toothbearing alveolar surface into small pairs of plates along ventral surface of the rostral appendage (p. 114).
83. Dorsal edge of anguloarticular notched by facet anterior to posterodorsal corner of the bone (p. 115) and flange on lateral commissure of prootic (p. 112).
84. Low number of dorsal spines resulting from loss of anterior elements in the series (p. 127).

Character 82 is the underlying synapomoprhy of this group and its division into a further 3 separate states (85, 88 & 89) clearly demarcates the *Macrognathus* species each from the other. *Macrognathus aculeatus* (species H) can be defined by the state of the group's synapomorphy, and by a 2nd apomorphic character:

85. Rostral toothplates usually in 38–55 pairs (p. 114).
86. Extremely large basisphenoid, associated with wide opening to posterior myodome (see Travers, 1984: 53 & fig. 30a & b).

The 10th node represents a single synapomorphy which indicates the closer relationship of *M. aral* (species I) and *M. siamensis* (species J) to one another than either is to *Macrognathus aculeatus*.

87. Deeply notched posterolateral margin of pterosphenoid forming anterior region of trigeminal foramen (see Travers, 1984: 65 & fig. 29a).

Macrognathus aral and *Macrognathus siamensis*, respectively, may be defined by the state of the group synapomorphy (i.e. 82) in each species:

88. Rostral toothplates: 14–28 pairs (p. 114).
89. Rostral toothplates: 7–14 pairs (p. 114).

The 11th node represents 4 synapomorphies uniting members of the 2nd branch of the main dichotomy (the 4th node in the cladogram). The synapomorphies uniting this assemblage, which includes all the African taxa but no others, are:

90. Lack of ascending process on urohyal or direct articulation between this bone and basibranchial 1 (p. 122).
91. Hypural plates, generally 2; tendency for parhypural fusion to ventral edge of lower plate; 8–10 principal fin rays and confluent caudal fin (p. 128).
92. Scapula foramen not completely bone enclosed (p. 125).
93. Tendency to have noticeably more caudal than abdominal vertebrae (p. 126).

Within this assemblage, 2 major subdivisions (K, and L to S in the cladogram) can be recognised. Subdivision K serves, for the time being, as a 'catch-all' assemblage for species united by the presence of synapomorphies 90–93. No other characters could be determined which would allow further subdivision of the group which, therefore, is represented as an unresolved polychotomy. Included in this group are *Mastacembelus albomaculatus, M. cunningtoni, M. ellipsifer, M. flavidus, M. frenatus, M. micropectus, M. moorii, M. ophidium, M. plagiostomus, M. platysoma, M. tanganicae, M. zebratus, M. congicus, M. shiranus, M. stappersii* and *M. vanderwaali.* A number of other nominal species (listed in Travers, 1984: table 1), for which material was unavailable should probably also be included.

The second major subdivision (L to S) is represented by the 12th node in the cladogram, and is defined by 2 synapomorphies:

94. No toothplate on pharyngobranchial 2 (p. 124).
95. Less than 5 preopercular sensory canal pores (p. 119).

Both these are loss features, and each has arisen separately, but never in combination (see p. 119 & 124), in several of the species lumped provisionally in species complex K. Since these characters are found in combination only in taxa L to S, they are taken to indicate the phylogenetic unity of the assemblage.

Group L to S (12th node in cladogram) can be subdivided into two sub-groups; L and M to S. L is a polychotomy (discussed on p. 123) of at least 15 species *viz: Mastacembelus batesii, M. brevicauda, M. flavomarginatus, M. goro, M. greshoffi, M. liberiensis, M. loennbergii, M. longicauda, M. marchii, M. marmoratus, M. niger, M. nigromarginatus, M. reticulatus, M. sclateri,* and *M. ubangensis,* and may possibly include several of the species for which study material was unavailable (see Travers, 1984: table 1). The second group contains species M to S, *viz*: *Mastacembelus paucispinis, M. brachyrhinus, M. brichardi, M. latens, M. crassus, M. aviceps* and the undescribed species (see p. 119).

Group L is defined by 2 synapomorphies:

96. Loss of anterior process on hypobranchial 3, and no ligamentous connection to basibranchial 2 (p. 124).
97. Arched ventral processes on basibranchial 2 (p. 123).

Although character 96 is a reductional one it is atypical of the condition in most outgroup taxa and is found in no other mastacembeloids. Therefore, it should be treated as a derived feature. Character 97 is a synapomorphic feature for this lineage. No other characters were found which would enable the interspecific relationships of these species to be resolved further, for the present they remain as an unresolved polychotomy.

This is not the case for the second group of the 12th dichotomy. Taxa in this branch are united by 3 synapomorphies represented by the 13th node, *viz*:

98. A reduction in the number of preopercular sensory canal pores (p. 119).
99. Loss of toothplate on hypobranchial 3 (p. 124).
100. A reduction in the number of caudal vertebrae (p. 126).

Although character 99 mimics the plesiomorphic condition, it is thought to be a secondary reduction that has arisen, independently, in some species recognised as part of polychotomy L (see p. 124). In combination, however, these characters are considered to be a unique synapomorphy suite for the species in which they occur (i.e. M to S).

Detailed analysis of the species in this group has led to the resolution of their interspecific relationships.

The 14th node in the cladogram represents 2 synapomorphies shared by *Mastacembelus paucispinis* and the undescribed *Mastacembelus* species. These are taken as indicative of the taxa being more closely related to one another than either is to any other species. These synapomorphies are:

101. Low number of dorsal spinous rays (their loss occurring posteriorly in the series), combined with a long soft rayed dorsal fin that extends across the junction between abdominal and caudal vertebrae (p. 127).

102. Tendency for the anterior tip of the prootic to form a bridge by contacting the ventral edge of a pedicel on the frontal (p. 111).

Although character 101 is a synapomorphy for both species, it can be separated into 2 states, each of which is species specific. Thus, *Mastacembelus paucispinis* (species M) can be defined by its having:

103. 7–10 dorsal spines (p. 127).

and the undescribed *Mastacembelus* species (N) by its having:

104. 15–16 dorsal spines (p. 127).

The 15th node in the cladogram represents 3 synapomorphies uniting the remaining 5 species, *viz*:

105. Loss of pleural ribs from the anterior abdominal vertebrae (p. 126).
106. Coronomeckelian very short (p. 115).
107. Part A_2 of the *adductor mandibulae* hypertrophied (p. 130).

These taxa can be considered a small species flock as they are endemic to the highly specialised rapids environment of the Lower Zaire River and conform to the prerequisite criteria discussed by Greenwood (1984). Of their features, 105 is a reductional one which does occur in some species provisionally assigned to species complex K (see p. 126). Whether this indicates that it has occurred independently in these various taxa or whether it indicates that the species in K may eventually be included in this group (O to S), cannot be determined at present.

Mastacembelus brachyrhinus (species O) may be distinguished from other species associated through node 15 by a single autapomorphic feature:

108. Dorsal expansion of the pterotic, associated with relatively small parietals, posterior expansion of frontals, and a tendency for the extrascapulae to be independent (p. 97).

The 16th node represents the following 4 synapomorphies:

109. Relatively large saccular bulla (accommodated entirely within the prootic, see p. 112).
110. Short anterior region of frontal; roofs small orbital cavity (see p. 113).
111. Endopterygoid very small and splinter-like (see p. 116).
112. Ventral limb of cleithrum short and indistinct (p. 125).
113. Tendency to be microphthalmic or cryptophthalmic (p. 113 & 130).

These synapomorphies unite *Mastacembelus brichardi* (species P), *Mastacembelus crassus* (species R) and *Mastacembelus aviceps* (species S), and probably *Mastacembelus latens* (species Q) as well, although lack of material precludes a definite allocation of this species. *Mastacembelus brichardi* may be distinguished from the other species by 2 autapomorphies, *viz:*

114. Loss of pigment (p. 85).
115. Eyes extremely small and lying medial to the *levator arcus palatini* muscle (see Travers, 1984: 125 & fig. 84b).

The remaining taxa in the lineage containing species M to S are *Mastacembelus crassus* (R), *M. aviceps* (S) and, probably, *M. latens* (Q).

The 17th node in the cladogram represents 6 synapomorphies for these species, *viz*:

116. Scaleless (p. 129).
117. Loss of basisphenoid (p. 110).
118. Anterior process of prootic very short or absent (p. 111).
119. Ectopterygoid with narrow anterolateral face (p. 118).

120. Dorsal opening of preopercular sensory canal on the posterior edge of preoperculum (p. 119).
121. Low 'keel' on basibranchial 1 (p. 121).

Mastacembelus latens is provisionally included in this group on the grounds that it shares one of these apomorphic characters (116). Until specimens of *M. latens* are available for dissection, the presence or absence of the other 5 synapomorphies cannot be determined.

The 6 synapomorphies shared by *Mastacembelus crassus* and *Mastacembelus aviceps* (and possibly *M. latens*) are all reductional ones. Several of these characters (all, apart from 120 & 121), or at least the tendency for their manifestation, are seen in *Pillaia* and in *Chaudhuria* (to a lesser extent). However, these taxa are clearly more closely related to *Mastacembelus sinensis* (as discussed on p. 128) and this complex of 6 characters in combination is an indicator of the close phyletic affinity of *M. crassus* and *M. aviceps*.

Mastacembelus crassus (species R) can be distinguished from *Mastacembelus aviceps* (S) by a single apomorphic character, *viz*:

122. Tendency for the trigeminal and facial foramina to be confluent (p. 111).

Whereas, *M. aviceps* can be identified by a combination of 5 apomorphic features, of which three are autapomorphic (i.e. 123, 124 & 125), *viz*:

123. Extremely small, splinter-like pterosphenoid lying along dorsolateral edge of frontal (p. 110).
124. Loss of neurocranial precommissural lateral wall and trigeminofacialis foramina (Travers, 1984: 68 & fig. 40a & b).
125. Anterior region of maxilla reduced to a weak and thin process tightly connected to premaxilla (p. 113).
126. Loss of ventral processes on basibranchial 2 (p. 123).
127. Hypurals fused into single fan-like plate (p. 128).

These characters, and that defining *M. crassus* are all reductional ones; one of them (character 127) also occurs in *Mastacembelus ellipsifer* (see p. 128), and is a further example of a reductional feature developing independently.

Proposed changes in classification

Comparison of the present state of mastacembeloid taxonomy (Fig. 18) with the phylogeny of the group (Fig. 20) reveals the necessity for numerous alterations to the existing classification, if the phylogenetic relationships of the species are to be reflected. These taxonomic and nomenclatural changes can be summarised as follows:

Re-allocation of the Mastacembeloidei from the Perciformes to the Synbranchiformes, as a sister taxon of the Synbranchoidei.

Expansion of the family Chaudhuriidae to incorporate two genera.

Elevation of *Mastacembelus sinensis* to a monotypic genus of the Chaudhuriidae.

The generic synonymy of *Chaudhuria* with *Pillaia* (and *Garo* see p. 109), but retention of both taxa as subgenera of *Chaudhuria*.

Division of the Mastacembelidae into two subfamilies (representing the Asian and African species, respectively).

Restriction of the *Mastacembelus* generic concept to five Asian and one Middle Eastern species only.

Expansion of the *Macrognathus* generic concept to include eight Asian species previously included in *Mastacembelus*.

Creation of a new subfamily for the African taxa.

Creation of new genera for the major African sublineages.

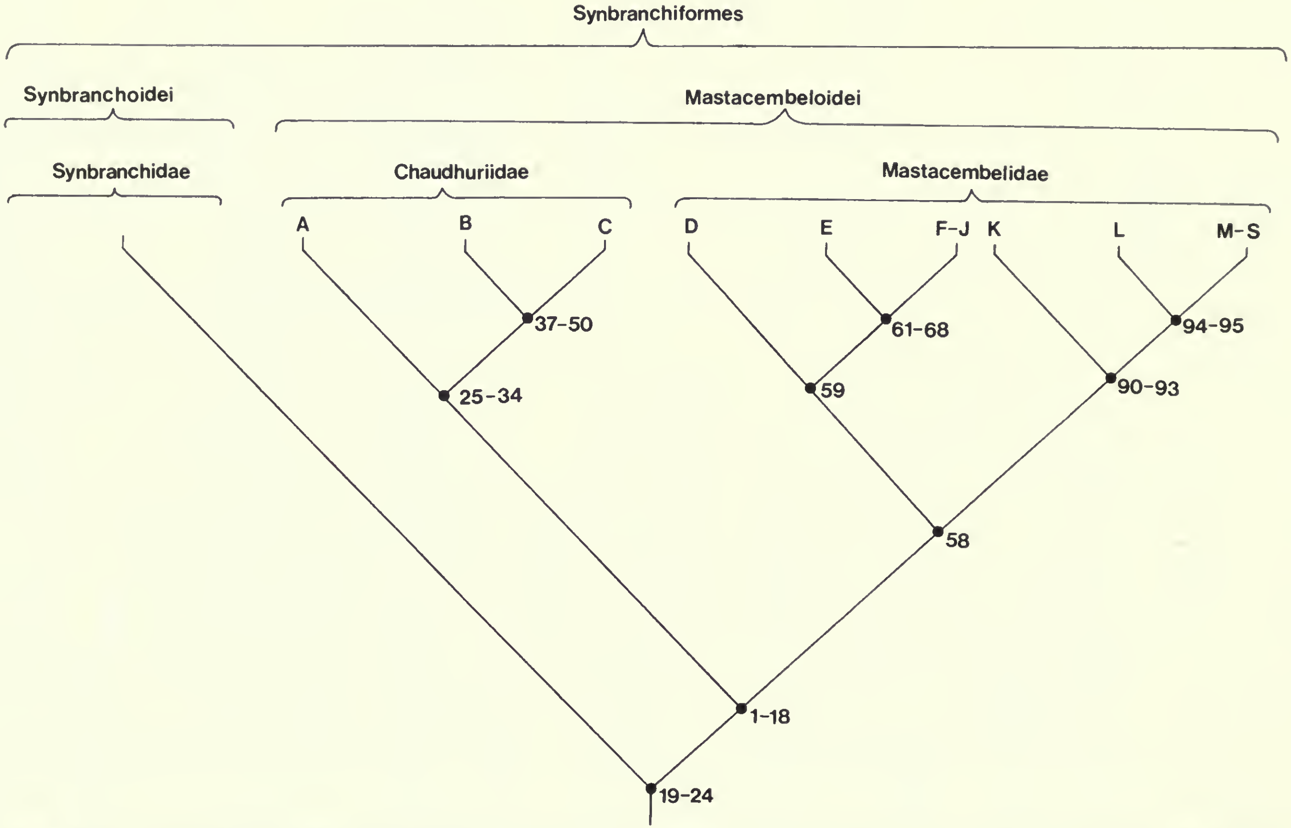

Fig. 20 Phylogeny of the Mastacembeloidei. Principal synapomorphies (given as a number) on which each node is based, and derived characters defining each of the terminal taxa A–S, are given in the text.

Diagnoses for the Synbranchiformes, its suborders, families, subfamilies and genera

Order **SYNBRANCHIFORMES** Berg 1940

Berg, L. S., 1940. Classification of fishes, both recent and fossil. *Trav. Inst. Zool. Acad. Sci. U.S.S.R.* **5:** 1–517, (English translation).

DIAGNOSIS. Eel-shaped acanthomorph fishes of small to moderate size (attaining max. length of approx. 1 m). Burrowing and cavernicolous habit commonly displayed. Lack pelvic fins or girdle, with caudal fin reduced or absent. Gill membrane attached to lateral wall of body by expansion of *hyohyoidei adductores* muscle; restricted opercular opening and insertion of *levator operculi* on lateral face of operculum. Prominent *adductor mandibulae* musculature, with part A_1 lying ventral to A_2, the latter tending to encroach across dorsal surface of neurocranium and into orbital cavity. Eyes small and well forward in skull. Anterior and posterior nostrils. Cycloid scales, small and oval, sometimes absent. Neurocranium attenuated, particularly precommissural region involving frontals, pterospenoid, vomer and parasphenoid; dorsal surface lacks crests or any form of sculpturing. Frontals turned down with prominent descending lamina. Infraorbital bones reduced apart from 1st. Palatines joined firmly to vomer in midline; generally tooth bearing. Vomer a long thin strut. Ectopterygoid articulates with lateral ethmoid, vomer or both. Non-protrusile upper jaw. Maxilla and premaxilla long and strut-like, with symphyseal and articulatory processes reduced or absent. Dentary with posterior extension along ventral edge of anguloarticular. Pectoral girdle remote from basicranium, posttemporal bone reduced (accompanied by loss of connection to pectoral girdle) or lost. Flexible craniovertebral joint. Dorsal gill arch skeleton positioned posteriorly; lacks first pharyngobranchial bone, with second pharyngobranchial reduced or absent. Numerous vertebrae.

Pantropical and subtropical fishes from freshwaters at high and low elevations; some individuals reported from brackish waters; tendency for facultative air breathing and sex reversal. 83 extant species currently recognised (no fossil record) in two suborders.

Suborder **SYNBRANCHOIDEI** Boulenger, 1904

Boulenger, G. A., 1904. A synopsis of the suborders and families of teleostean fishes. *Ann. Mag. nat. Hist.* (7), **13:** 161–190.

DIAGNOSIS. Monotypic suborder with synbranchiform features given above. For annotated account of groups, species diagnoses and key see Rosen & Greenwood (1976: 49–66).

Suborder **MASTACEMBELOIDEI** Greenwood *et al*, 1966

Greenwood, P. H., Rosen, D. E., Weitzman, S. H. & Myers, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms.
Bull. Am. Mus. nat. Hist. **131:** 339–456.

OPISTHOMI Boulenger, G. A., 1904. *Ann. Mag. nat. Hist.* (7), **13:** 161–190. (subordinal rank).
Regan, C. T., 1912. *Ann. Mag. nat. Hist.* (8), **9:** 217–219 (ordinal rank).
MASTACEMBELIFORMES Berg, L. S., 1940. *Trav. Inst. Zool. Acad. Sci. U.S.S.R.* **5:** 1–517.

DIAGNOSIS. Synbranchiform fishes with long dorsal and anal fin composed of isolated spinous rays anterior to long series of soft branched rays. Rostral appendage formed from anterior nostrils (at end of tubular extensions) positioned lateral to a central rostral tentacle. Rim of anterior nostril generally with two wide (fimbrules) and two narrow (fimbriae) flaps of skin. '*Musculus intraoperculi*' differentiated within opercular series. Elongate ethmovomerine region with long nasal and 1st infraorbital bones. Preorbital spine (posterior tip of 1st infraorbital) generally pierces skin. Tubular lateral ethmoids accommodate anterior end of massive *nervus olfactorius*. Pterosphenoids, joined firmly in midline; frontals completely enclose foramen magnum. Small compressed basisphenoid, occasionally absent. Anterior regions of prootic and sphenotic attenuated; former having long process extending into orbital cavity and latter having wide lateral flange. Saccular bulla generally small and house entirely within the prootic. Extrascapulae (lateral and medial) lost and sensory canal enclosed by parietal. 'Ball and socket' craniovertebral joint. *Obliquus superioris* with anterior insertion on posterior edge of exoccipital. Posterior end of Baudelot's ligament forked. Very large coronomeckelian dorsal to dentary, across lateral face of suspensorium. Pair of ventral processes on basibranchial 2. Hypobranchial 3 with a round toothplate fused to dorsal surface. Pseudobranch present.

Ethiopian and Oriental distribution. Wide range in tropical and subtropical Africa, and in Asia continuously from Middle East to islands of Indonesia, and eastern China seaboard. 68 species currently recognised, in two families.

Family **CHAUDHURIIDAE** Annendale, 1918

Annendale, N., 1918. Fish and fisheries of the Inle Lake. *Rec. Ind. Mus.* **14:** 33–64.

TYPE GENUS. *Chaudhuria* Annendale, 1918.

DIAGNOSIS. Derived mastacembeloid fishes with above features but tending to small adult size and reduction or loss of many characters by heterocrony. Rostral appendage reduced or lost. Needle-like parasphenoid posterior processes. Dorsomedial region of exoccipital with perforated dorsal surface and separated from opposite number. 1–2 inner rows of premaxillary teeth. Ectopterygoid with narrow lateral face and very long antero-dorsal process. Palatine reduced in size (lacks suborbital flange). Three or fewer epicentral ribs. Interdigitating processes of anterior and posterior ceratohyals reduced or lost. No endopterygoid, basibranchial 2 ventral processes or epipleural ribs.

Confined to China (including Taiwan and possibly Korea), Thailand, Burma and northern India. Family expanded to incorporate 4 species in two genera.

Genus ***RHYNCHOBDELLA*** Bloch & Schneider, 1801

Blotch, M. E. & Schneider, J. G., 1801. M. E. Blochii Systema Ichthyologiae iconibus ex illustratum. Post oblitum auctoris opus inchoatum absolvit, correxit, interpolavit . . . J. G. Schneider, Saxo. Berolini.

TYPE SPECIES. *Rhynchobdella sinensis* Bleeker, 1870

DIAGNOSIS. Monotypic chaudhuriid genus. Parietals may contact medially; very large 3rd anal spine equal in size to the 2nd spine and separated from it by four vertebrae. Tip of vertical urohyal ascending process contacts underside of basibranchial 2.

Widely distributed in China, Taiwan and possibly N. & S. Korea.

Genus ***CHAUDHURIA*** Annendale, 1918

Annendale, N., 1918. Fish and fisheries of the Inle Lake. *Rec. Ind. Mus.* **14:** 33–64.
Pillaia Yazdani, G. M., 1972. *J. Bombay Nat. Hist. Soc.* **69**(1): 134–135; Talwar, P. M., Yazdani, G. M. & Kundu, D. K., 1977. *Proc. Indian Acad. Sci.* **85:** 53–6.
Garo Yazdani, G. M. & Talwar, P. M., 1981. *Bull. zool. Surv. India* **4**(3): 287–288.

TYPE SPECIES. *Chaudhuria caudata* Annendale, 1918

DIAGNOSIS. Highly derived chaudhuriid fishes with particularly small adult size (generally between 40–60 mm.). Extreme reduction of many features appears to mimic plesiomorphic condition e.g. large saccular bulla partly within prootic, exoccipital and basioccipital, coronomeckelian reduced to a small ossicle on medial face of anguloarticular. Loss of numerous features including; pterosphenoid, basisphenoid, frontal ventral lamina, cephalic sensory canal system (reduced or lost), palatine, pharyngobranchial 2 toothplate, dorsal and anal spines, and scales. Lack of ectopterygoid articulation with lateral ethmoid (ectopterygoid directly contacts lateral face of vomerine shaft); possibly associated with loss of palatine. Posterior end of vomer ventrally depressed; pars jugularis pierced by single relatively large foramen.

Three species confined to Thailand, Burma and northern India:
Chaudhuria caudata Annendale, 1918
Chaudhuria indica (Yazdani), 1972
Chaudhuria khajuriai (Talwar, Yazdani & Kundu), 1977.

Family **MASTACEMBELIDAE** Günther, 1861

Günther, A., 1861. Catalogue of the acanthopterygian fishes. **3.** London.

TYPE GENUS. *Mastacembelus* Scopoli, 1777

DIAGNOSIS. Mastacembeloid fishes with features as for the suborder (given above) and, additionally: wide separation of hyomandibula and metapterygoid, associated with large symplectic.

64 species widespread throughout the range of the suborder. Two subfamilies comprise the mastacembeloids Oriental and Ethiopian regions.

Subfamily **MASTACEMBELINAE** subfam. nov.

TYPE GENUS. *Mastacembelus* Scopoli, 1777

DIAGNOSIS. Mastacembelid fishes with distinct caudal fin generally unconnected to posterior ray of dorsal or anal fin. If connected (by membrane) caudal fin rays extend posterior to, and remain distinct from, last posterior dorsal and anal fin ray. Caudal fin skeleton with 4 separate and autogenous hypural plates. Rostral appendage varies from very large to intermediate size. Tendency to be brightly coloured.

17 species widely distributed from Middle East to SE. Asia including China and continental islands of Indonesia, arranged in two genera.

Genus ***MASTACEMBELUS*** Scopoli, 1777

Scopoli, J. A., 1777. Introductio ad Historiam Naturalem, Prague.

TYPE SPECIES. *Mastacembelus mastacembelus* (Banks & Solander, in Russell), 1794; See Wheeler, 1955.

DIAGNOSIS: Mastacembeline fishes of moderate to large size (over 50 cm.). Attenuated anterior arm of endopterygoid lies between ectopterygoid and lateral ethmoid connection. Neurocranium broad with rostral appendage of moderate size.

6 species, five widely distributed in SE. Asia including the continental islands of Indonesia:
Mastacembelus alboguttatus Boulenger, 1893
Mastacembelus armatus (Lacépède), 1800
Mastacembelus erythrotaenia Bleeker, 1870
Mastacembelus oatesii Boulenger, 1893
Mastacembelus unicolor (Kuhl & van Hasselt) Cuv. & Val., 1831

and the single Middle Eastern species:
Mastacembelus mastacembelus (Banks & Solander, *in* Russell), 1794.

Genus ***MACROGNATHUS*** Lacépède, 1800

Lacépède, B., 1800. *Histoire naturelle des poissons.* Paris 2.

TYPE SPECIES. *Ophidium aculeatum* Bloch, 1786

DIAGNOSIS. Mastacembeline fishes of moderate to small size (under 50 cm.). Deep bodied with elongate, narrow neural and haemal spines. Rostral appendage large and more elongate than in other mastacembeloids. Six slender and digitiform fimbriae surround rim of each anterior nostril. Distinct anterior part of *adductor arcus palatini* muscle inserts on attenuate posterior edge of 1st infraorbital. Narrow, but deep, neurocranium with dorsal surface of frontals sloping ventrally; ventrolateral face of exoccipital and posteroventral margin of basioccipital expanded. Posterior region of parasphenoid undivided (apart from tip) and excavated to form pit-like depression on ventral surface of basicranium (for muscle attachment). Deep basioccipital fossa accommodates anterior end of Baudelot's ligament. Vertebral count relatively low. In addition, see diagnosis given by Roberts (1980: 387). Roberts' (1980) *Macrognathus* generic concept (i.e. *Macrognathus aculeatus, M. aral* and *M. siamensis*) now expanded to include eight Oriental species previously assigned to *Mastacembelus* (i.e. *'Mastacembelus' caudiocellatus, 'M'. circumcinctus, 'M'. guentheri, 'M'. keithi, 'M'. maculatus, 'M'. pancalus, 'M'. perakensis* and *'M'. zebrinus*).

11 species widely distributed in SE. Asia and continental islands of Indonesia:

Macrognathus aculeatus (Bloch), 1786
Macrognathus aral (Bloch & Schneider), 1801; see Roberts, 1980
Macrognathus siamensis (Günther), 1861; see Roberts, 1980
Macrognathus caudiocellatus (Boulenger), 1892
Macrognathus circumcinctus (Hora), 1924
Macrognathus guentheri (Day), 1865
Macrognathus keithi (Herre), 1940
Macrognathus maculatus (Cuv. & Val.), 1831
Macrognathus pancalus Hamilton Buchanan, 1822
Macrognathus perakensis (Herre & Myers), 1937
Macrognathus zebrinus (Blyth), 1859

Subfamily **AFROMASTACEMBELINAE** subfam. nov.

TYPE GENUS. *Afromastacembelus* gen. nov.

DIAGNOSIS. Mastacembelid fishes with confluent caudal fin rays continues with posterior rays of dorsal and anal fin. Caudal fin skeleton generally with two separate and autogenous hypurals, tend to have parhypural fused to lower edge of ventral element and to have only 8–10 principal fin rays. Loss of ascending process on urohyal and direct articulation between urohyal and basibranchial 1. Scapula foramen not completely bone enclosed. Tendency to have noticeably more caudal than abdominal vertebrae.

This subfamily represents the Ethiopian mastacembelid species widely distributed throughout tropical and subtropical regions of the continent. 46 species currently recognised and provisionally arranged in two genera.

Genus ***CAECOMASTACEMBELUS*** Poll, 1958

Poll, M., 1958. Description d'un poisson aveugle nouveau du Congo Belge appartenant à la famille des Mastacembelidae. *Revue Zool. Bot. Afr.* **57**: 388–392.

TYPE SPECIES. *Caecomastacembelus brichardi* Poll, 1958

DIAGNOSIS. Afromastacembeline fishes of small to moderately large size. With no pharyngobranchial 2 toothplate and less than five preopercular sensory canal pores. Species with atrophied eye tissues and one (i.e. type for genus) is anoptic. General morphological simplification (by secondary reduction and loss) occurs in microphthalmic and cryptophthalmic species (parallels condition in *Chaudhuria,* although not carried to such extremes).

Distributed predominently in western half of continent and includes small species flock endemic to lower Zairean rapids. At least 22 species tentatively assigned to this genus, and probably several more, for which study material was unavailable (see Travers, 1984: table 1):

Caecomastacembelus aviceps (Roberts & Stewart), 1976
Caecomastacembelus batesii (Boulenger), 1911
Caecomastacembelus brachyrhinus (Boulenger), 1899
Caecomastacembelus brevicauda (Boulenger), 1911
Caecomastacembelus brichardi Poll, 1958

Caecomastacembelus crassus (Roberts & Stewart), 1976
Caecomastacembelus flavomarginatus (Boulenger), 1898
Caecomastacembelus goro (Boulenger), 1902
Caecomastacembelus greshoffi (Boulenger), 1901
Caecomastacembelus latens (Roberts & Stewart), 1976
Caecomastacembelus liberiensis (Steindachner), 1894
Caecomastacembelus loennbergii (Lönnberg), 1895
Caecomastacembelus longicauda (Boulenger), 1907
Caecomastacembelus marchii (Sauvage), 1892
Caecomastacembelus marmoratus (Perugia), 1892
Caecomastacembelus niger (Sauvage), 1878
Caecomastacembelus nigromarginatus (Boulenger), 1898
Caecomostacembelus paucispinis (Boulenger), 1899
Caecomastacembelus reticulatus (Boulenger), 1911
Caecomastacembelus sclateri (Boulenger), 1903
Caecomastacembelus ubangensis (Boulenger), 1911
Caecomastacembelus sp.

and probably:

Caecomastacembelus ansorgii (Boulenger), 1905
Caecomastacembelus cryptacanthus (Günther), 1867
Caecomastacembelus laticauda (Ahl), 1937
Caecomastacembelus sanagali (Thys van den Audenaerde), 1972
Caecomastacembelus seiteri (Thys van den Audenaerde), 1972

Genus ***AFROMASTACEMBELUS*** gen. nov.

TYPE SPECIES. *Mastacembelus tanganicae* Günther, 1893

DIAGNOSIS. Afromastacembeline fishes of moderate to large size; occur predominently from eastern half of continent and include species endemic to Lake Tanganyika. All afromastacembeline species, other than those assigned to *Caecomastacembelus,* provisionally lumped in this 'catch-all' assemblage (which may not be monophyletic) pending closer examination of groups interspecific relationships.

At least 16 species tentatively placed in this genus, and probably several more, for which study material was unavailable (see Travers 1984: table 1).

Afromastacembelus albomaculatus (Poll), 1953
Afromastacembelus congicus (Boulenger), 1896
Afromastacembelus cunningtoni (Boulenger), 1906
Afromastacembelus ellipsifer (Boulenger), 1899
Afromastacembelus flavidus (Matthes), 1962
Afromastacembelus frenatus (Boulenger), 1901
Afromastacembelus micropectus (Matthes), 1962
Afromastacembelus moorii (Boulenger), 1898
Afromastacembelus ophidium (Günther), 1893
Afromastacembelus plagiostomus (Matthes), 1962
Afromastacembelus platysoma (Poll & Matthes), 1962
Afromastacembelus shiranus (Günther), 1896
Afromastacembelus stappersii (Boulenger), 1914
Afromastacembelus tanganicae (Günther), 1893
Afromastacembelus vanderwaali (Skelton), 1976
Afromastacembelus zebratus (Matthes), 1962

and probably:

Afromastacembelus moeruensis (Boulenger), 1914
Afromastacembelus signatus (Boulenger), 1905
Afromastacembelus trispinosus (Steindachner), 1911

The revised classification can be summarised as follows:
Series: Percomorpha (consists of 12 orders)
Order: Synbranchiformes
  Suborder: Synbranchoidei
    Family: Synbranchidae (see Rosen & Greenwood, 1976)
  Suborder: Mastacembeloidei
    Family: Chaudhuriidae
      Rhynchobdella
      Chaudhuria
    Family: Mastacembelidae
      Subfamily: Mastacembelinae
        Mastacembelus
        Macrognathus
      Subfamily: Afromastacembelinae
        Caecomastacembelus
        Afromastacembelus

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Tilapiine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

The tilapias are cichlid fishes of Africa and the Levant that have become the subjects of fish-farming throughout the warm countries of the world. This book described 41 recognized species in which one or both parents carry the eggs and embryos in the mouth for safety. Substrate-spawning species, of the now restricted genus *Tilapia*, are not treated here.

Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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A review of the anatomy, taxonomy, phylogeny and biogeography of the African neoboline cyprinid fishes

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Introduction

In a review of the bariliine cyprinids (Howes, 1980), the genus *Engraulicypris* which previously had contained ten species was recognized as monotypic, its only species, *E. sardella* confined to Lake Malawi. Those species formerly included in *Engraulicypris* were re-assigned to the genera *Neobola* Vinciguerra, *Chelaethiops* Boulenger, and *Rastrineobola* Fowler, with the accompanying statement that they formed a monophyletic assemblage whose close relationships were with Asian phoxinines rather than with African bariliines (Howes, 1980 : 196). Later, Howes (1983) modified these views and included *Neobola, Chelaethiops* and *Rastrineobola* among the bariliines, naming them as the neoboline lineage (see fig. 2 in Howes, 1983). Although a suite of supposed apomorphies characterizing the three genera were given (Howes, 1980 : 195), together with lists of their contained species no detailed generic diagnoses were presented. The purposes of this paper are:

1. To give diagnoses of the genera *Neobola, Chelaethiops* and *Rastrineobola* and establish a new genus to contain two species formerly assigned to *Neobola.* The characters used in these diagnoses are, for the greater part, those involving cranial anatomy. From previous studies (Howes, 1978; 1979; 1980; 1981; 1982; 1983) and from out-group comparisons made in the course of this work it is clear that in cyprinids cranial characters provide the most pertinent information at all levels of investigation.

2. To review the taxonomy of the included species. Although the neoboline cyprinids are abundant in many lakes and rivers of east, central and west Africa, they are, as compared with other cyprinids poorly represented in collections both in terms of sample sizes and geographic range. The species are small-sized, pelagic zooplanktivores and form an important part of the diet of many piscivores (see Fryer & Iles, 1972; Lowe-McConnell, 1975; van Oijen, 1982). Previous taxonomic reviews have been those of Poll (1945) and Whitehead (1962) but these authors relied for the most part on data compiled from the literature. Almost

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all the material on which this review is based is from the collections in the British Museum (Natural History), and types of nearly all species have been examined. Other specimens used are from the collections of the Central African Museum in Tervuren (MRAC) and the American Museum of Natural History (AMNH).

3. To confirm the supposed monophyly of the neoboline genera and to consider their intra- and interrelationships.

4. To consider, in the light of their phylogenetic relationships, the biogeography of the neoboline taxa and some broader issues of African biogeography.

Diagnoses, anatomy and taxonomy of the neoboline genera

NEOBOLA Vinciguerra, 1895

Neobola is characterized by the articulation of the lower jaw extending posterior to the centre of the orbit; a dorsally channelled, broad supraethmoid; 10–12 olfactory lamellae on each half of the nasal rosette; 4–7 short gill-rakers on 1st ceratobranchial; small pectoral axial scale with a fleshy ventral border; pharyngeal teeth in two rows, 5·3; scales small with 5–8 parallel radii, 37–41 in the lateral line; the lateral line gently decurved anteriorly and running close to the ventral margin of the trunk with a wave-like irregularity along the caudal peduncle; swimbladder divided by a deep constriction into short anterior and posterior chambers, the posterior extending to above the pelvic fin.

CONTAINED SPECIES. *N. bottegi, N. fluviatilis* and *N. stellae.*

Cranial anatomy

Osteology (Figs 2–4). The *ethmo-vomerine bloc* is short, deep and triangular, its anterior border has a sloped indentation. The supraethmoid is narrow-waisted, the lateral margins of the bone are concave and raised, thereby forming a shallow dorsal channel; the frontals overlay the posterior border of the bone. The vomer has a concave anterior border which projects only slightly beyond the overlying mesethmoid. Each lateral ethmoid is truncated with the dorsal part of the lateral wall extending anteriorly (Fig. 4).

The *frontal sensory canal* runs along the margin of that bone and is raised above the level of the supraorbital. There are 4 or 5 sensory canal pores; the first is extensive, and all open somewhat laterally. The *nasal* is long and curved into the concavity of the supraethmoid border; it has no dorsal pores.

The *infraorbitals* are deep (Fig. 6), the sensory canal of the 1st runs along the ventral border of the bone, but in the 2nd, 3rd and 4th the canal runs along the orbital border. In the 5th, the canal passes through the centre of the bone. The *supraorbital* is broad and long, narrowly separated from the 5th infraorbital.

The *orbitosphenoids* are connected with the parasphenoid *via* a narrow septum; the *pterosphenoid* contacts the ascending process of the parasphenoid across a narrow area of bone. There is a small lateral *sphenotic* process which provides the greater part of the dilatator fossa. The *prootic* is large with the anterior trigemino-facialis foramen narrowly separated from its anterior border; there is a long lateral commissure. The posterior myodome is completely floored by the parasphenoid and basioccipital. A small posttemporal fossa is formed by the posterior separation of the *dermo* and *autopterotics.* The *supraoccipital* is small, lacks a crest, and is confined to the posterior slope of the cranium.

The *jaws* are long, the posterior tip of the maxilla extends to, or beyond the centre of the orbit. The maxilla is slender with a low mid-lateral (palatine) ascending process which curved laterally (Fig. 7). The posterior part of the maxilla is spine-like with only a slightly expanded tip which extends to below the centre of the orbit. The premaxilla is slender with a low ascending process and slightly concave ventral border. The dentary is shallow with a long, high, backwardly sloped coronoid process; the dorsal margin of the dentary is gently convex (Fig. 8). The anguloarticular is short with a slightly concave dorsal border.

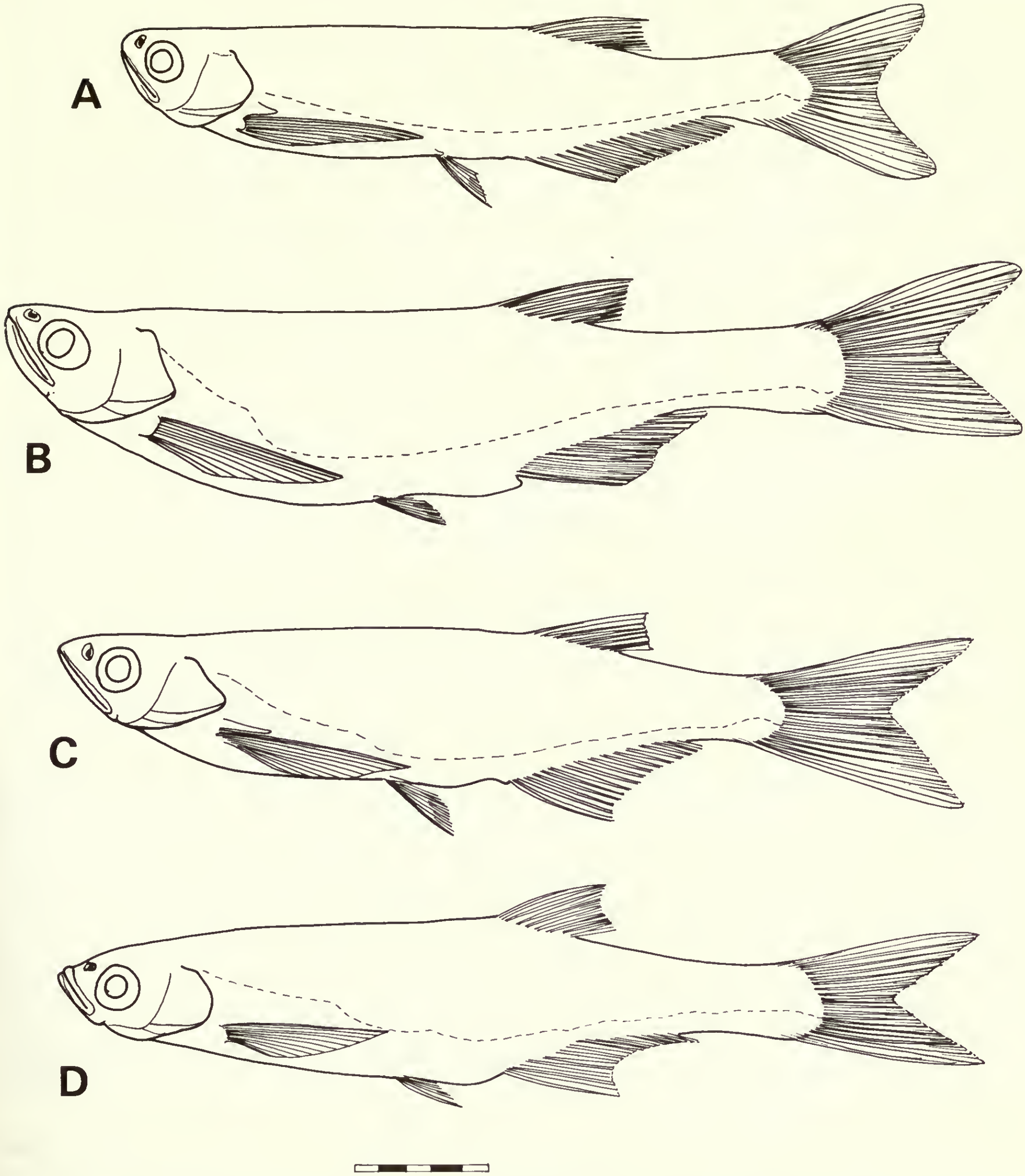

Fig. 1 Representatives of neoboline genera: A, *Neobola bottegi;* B, *Mesobola brevianalis*; C, *Chelaethiops bibie;* D, *Rastrineobola argentea* (drawn from a Lake Kioga specimen). All genera have 7 branched dorsal fin rays (rarely 6 or 8) I 10 pectoral rays; I 7 pelvic rays and 10+9 principal caudal rays.

Suspensorium (Fig. 9). The hyomandibula is broad and its dorsal facets are deeply separated. There is a weak lateral flange, its recess providing the insertion of the *levator arcus palatini* muscle. The ento- and metapterygoids have a marked concavity toward the midline; the dorsal border of the entopterygoid is straight, that of the metapterygoid is markedly concave. The palatine is laterally compressed, its anterior head forming a tripartite process, the medial spur of which overlies the concavity between the mid-lateral and anterior ascending maxillary processes.

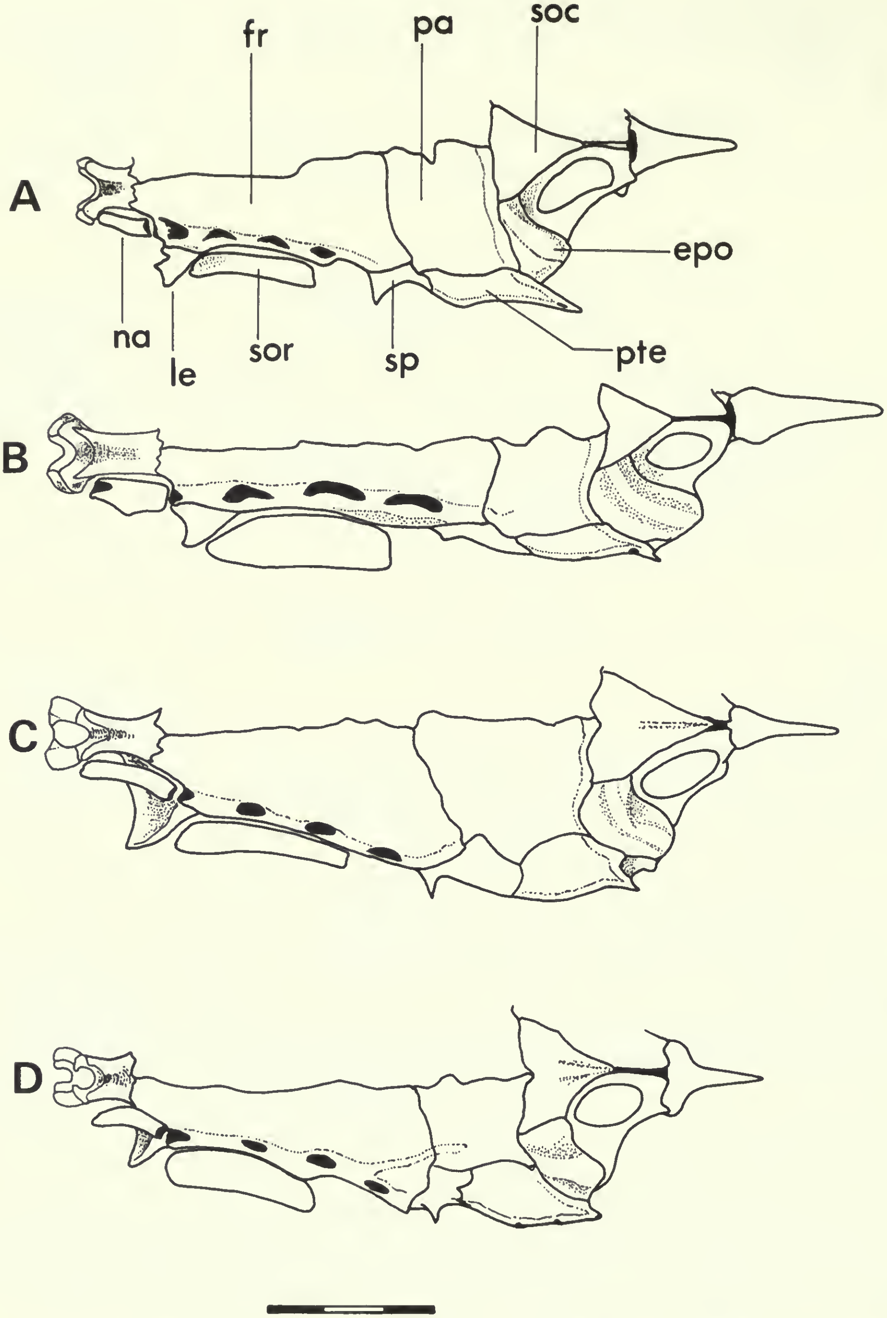

Fig. 2 Crania, in dorsal view: A, *Neobola bottegi;* B, *Chelaethiops elongatus*; C, *Mesobola brevianalis*; D, *Rastrineobola argentea.* epo = epioccipital; fr = frontal; le = lateral ethmoid; na = nasal; pa = parietal; pte = dermopterotic; soc = supraoccipital; sor = supraorbital.

Branchial arches. The ceratobranchials bear 4–8 short gill-rakers. Pharyngeal teeth on the 5th ceratobranchial are caniniform, arranged in two rows (5.3).

The *operculum* (Fig. 9) has a shallow concave posterior border, the ventro-posterior part of the bone being attenuated.

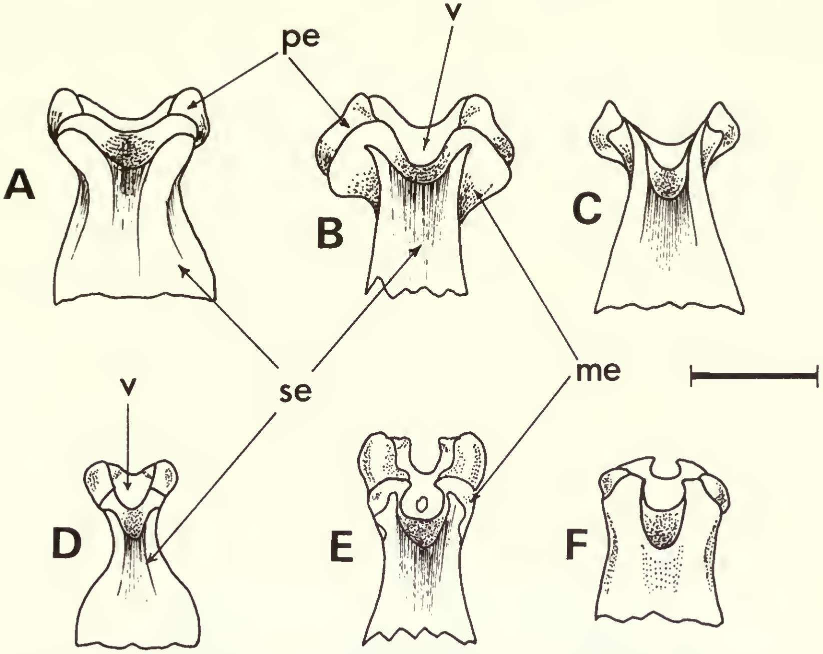

Fig. 3 Ethmoid region in dorsal view: A, *Neobola bottegi*; B, *Chelaethiops elongatus*; C, *C. bibie*; D, *Mesobola brevianalis*; E, *Rastrineobola argentea*; F, *Leptocypris niloticus*. me = mesethmoid; pe = preethmoid; se = supraethmoid; v = vomer. Scale = 1 mm.

Myology (Fig. 13). Section A_1 of the *adductor mandibulae* muscle originates from the quadrate and preoperculum. There are two divisions of the section. (1), a triangular anterior part, A_1*ant*, which has an aponeurotic constriction below the anterior border of the eye and is bordered by the ligamentum primordium. This anterior segment continues along the maxilla as a narrow, parallel-fibred element and inserts below the outwardly curved palatine process of the maxilla; (2) a posterior part, A_1*post*, extending from the preoperculum to insert partly on the rictal tissue and partly onto the rim of the dentary coronoid process. Muscle A_2 is thin and narrowly triangular, inserting into an aponeurosis medial to the anguloarticular; a small A_w section originates from the aponeurosis.

The *levator arcus palatini* is divided by the sphenotic process and inserts onto the lateral hyomandibular flange. The *dilatator operculi* is small and broadly triangular, originating from the sphenotic spur and inserting onto the small opercular process.

Pectoral girdle (Fig. 10)

The upright part of the cleithrum is short, the posterior lamellae lacking any central process; the tip of the horizontal limb extends to a point below the parasphenoid ascending process; the supracleithrum is short, articulating halfway along the cleithral limb; the coracoid is shallow with a fretted anterior border. There is no postcleithrum.

Vertebral column

The 1st vertebra has a flat articulatory face, it bears short lateral processes that are directed somewhat anteriorly. Centra 2 and 3 are fused and bear long, slightly posteriorly curved lateral processes. The caudal fin skeleton (Fig. 17A). has 6 hypurals, the 6th being minute. The fused preural and ural centra (PU1 + U1) bear a small neural spine; the epural is long and slender; paired uroneurals are lacking. The parhypural bears a short but wide hypurapophysis. Dorsal and ventral procurrent rays are well-developed.

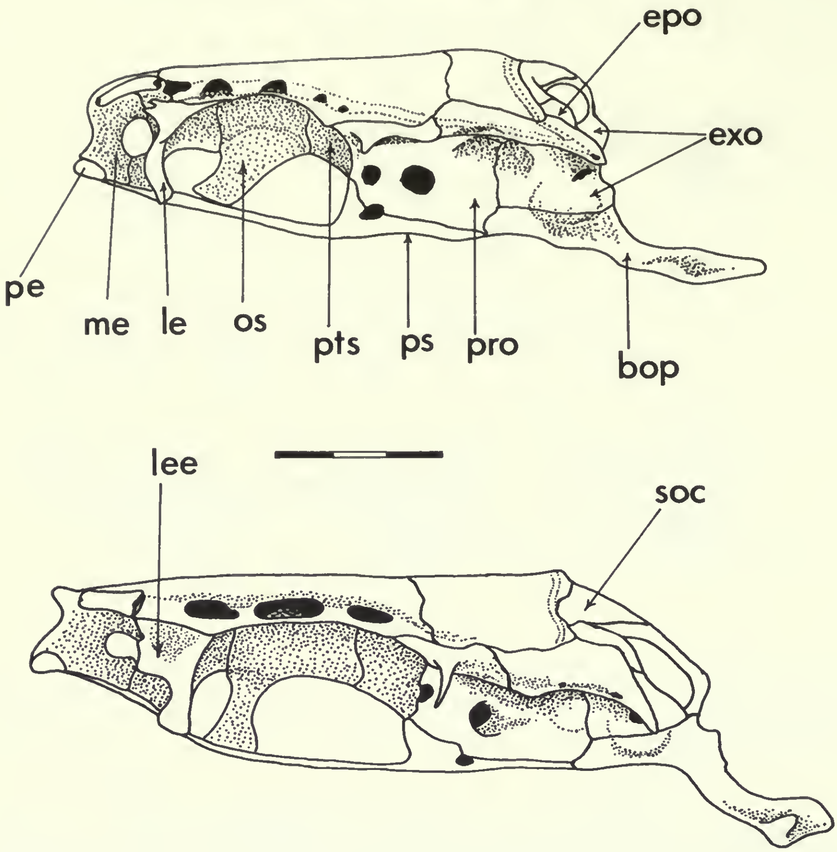

Fig. 4 Crania, in lateral view, (above) *Neobola bottegi* and (below) *Chelaethiops elongatus.* bop = basioccipital process; exo = exoccipital; lee = lateral ethmoid extension; os = orbitosphenoid; pro = prootic; ps = parasphenoid; pts = pterosphenoid; other abbreviations as in previous figs.

Taxonomy

Three species are assigned to *Neobola, N. bottegi* Vinciguerra, 1895; from the Webei Shebeli and Omo rivers; *N. fluviatilis* (Whitehead), 1962 from the Athi and Tana rivers, Kenya and *N. stellae* (Worthington), 1932 from Lake Turkana, Kenya.

Whitehead (1962) separated *Neobola fluviatilis* from *N. bottegi* on its having fewer lateral line scales and a higher number of branched anal fin rays. However, I find there to be no substantial differences in these features. There are 37–40 lateral line scales in *N. bottegi cf.* 38–40 in *N. fluviatilis.* Anal fin rays range in *N. bottegi* from 14–18 (N14) *cf.* 19–21 (N18) in *N. fluviatilis.* Gill-raker counts similarly have a continuous range; 5–8 in *N. bottegi* (7 and 8 in specimens from the Webi Shebeli River and 5–6 in other specimens from other localities listed below) *cf.* 4–6 in *N. fluviatilis.* In both species there are 12 nasal lamellae on each half rosette. There are, however, differences in the morphology of the pectoral axial scale, it being smaller and more lobate in *N. fluviatilis* than in *N. bottegi.* Pharyngeal teeth in both species are in 2 rows, 4.3 or 5.3 in *N. bottegi* and 4.2 in *N. fluviatilis.* The total vertebral number for both species is 40 or 41 (4 Weberian + 14 abdominal + 21–22 caudal + the fused preural and ural centrum). It seems likely that *N. fluviatilis* is but the southern population of *N. bottegi;* further collections from northern Kenya and southern Ethiopia should help resolve this problem.

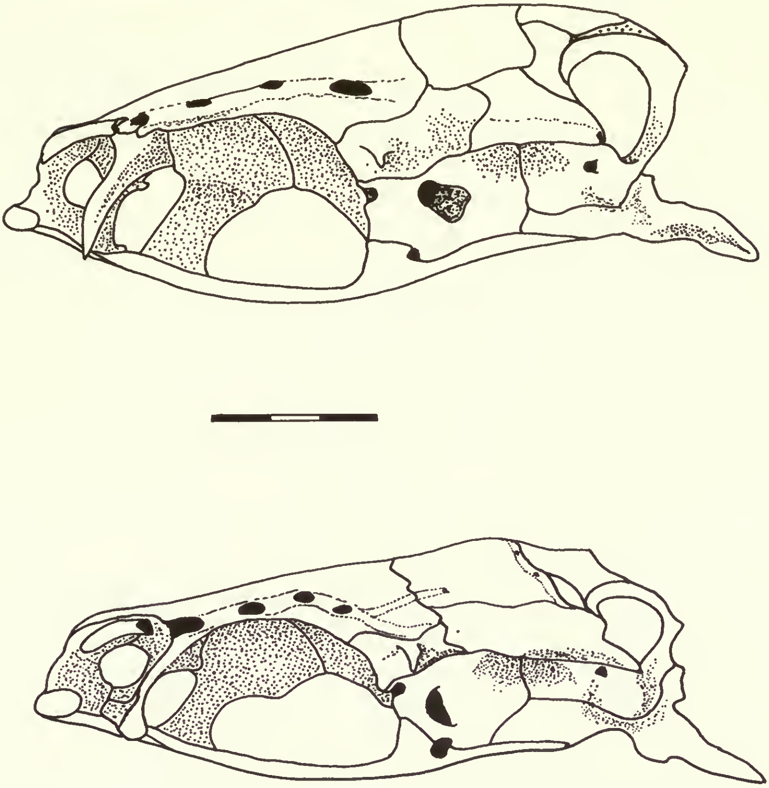

Fig. 5 Crania, in lateral view, (above) *Mesobola brevianalis* and (below) *Rastrineobola argentea.*

Neobola stellae (Worthington), 1932 is distinguished from *N. bottegi* and *N. fluviatilis* by its small size (maximum adult size measured, 25 mm SL), lower number of olfactory lamellae (10 on each half rosette), lower vertebral number (total, 37 or 38 *cf.* 40–41) and a small, bluntly triangular pectoral axial scale. There are 28–33 lateral line scales. Worthington (1932) gives a count of 34–37, but in fact none of the types have more than 34 lateral line scales even if one includes scales at the base of the caudal fin. Branched anal fin rays number 12–18. Pharyngeal teeth are in 2 rows, 4.2.

SPECIMENS EXAMINED. *Neobola bottegi;* 1902.11.7:22, Imi, Webi Shebeli; 1905.7.25:94–5, Modjo R.; 1905.7.251:110–112, Wabbi R.; 1905.7.25:106–9, Iraro R.; 1950.11.25:5–6, Webi Shebeli; 1982.5.17:9–14, Webi Shebeli. *Neobola fluviatilis*; 1961.5.3:1 (holotype); 2–6 (paratypes), Athi R. near Kithimani; 1966.7.5:29–42, Athi R. at Yalta: 1966.8.25:6, Tana R. *Neobola stellae*; 1932.6.13:57–65 (syntypes); 1932.6.13:47–56, all labelled 'Lake Rudolf'; 1973.8.6:65–76, Loiengalani; 1981.12.17:2488–2587, Lodge Spit; 1981.12.17:2173–82, Ferguson's Gulf, Lake Turkana.

CHELAETHIOPS Boulenger, 1899

Chelaethiops is characterized by its pointed snout and long, shallow jaws, the articulation of the lower jaw extending posterior to the centre of the eye, a dorsally channelled broad to narrow supraethmoid, laterally opening frontal pores, 16–26 olfactory lamellae on each half rosette, few (5) to many (18) gill-rakers on 1st ceratobranchial, elongate pectoral axial scales, pharyngeal teeth long, recurved in three rows, 5.3.2. Scales with 7–9 widely

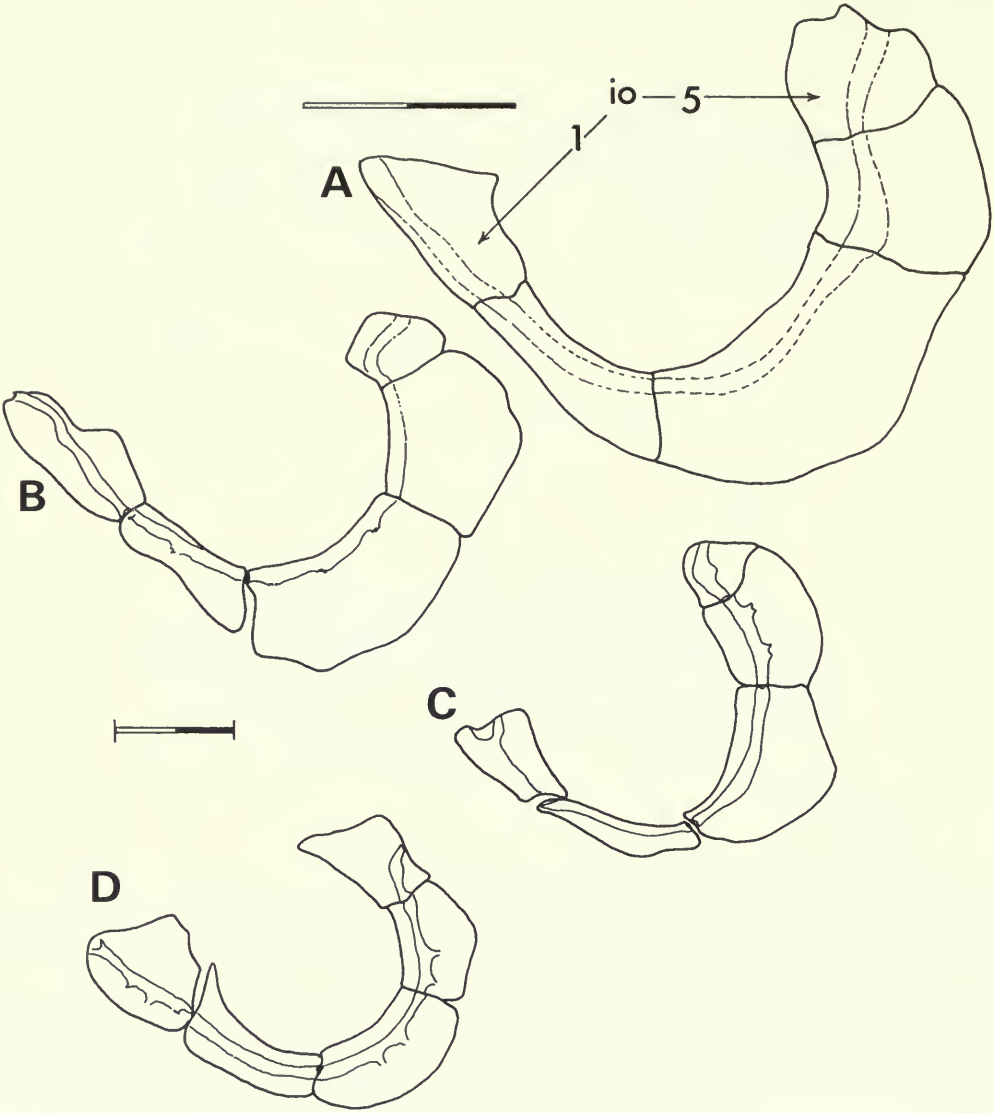

Fig. 6 Infraorbital bones: A, *Neobola bottegi;* B, *Chelaethiops bibie*; C, *Mesobola brevianalis*; D, *Rastrineobola argentea.*

spaced radii, 36–42 lateral line scales; the lateral line gently decurved anteriorly and with a pronounced curve above the pelvic fin base, often with a wave-like irregularity along the caudal peduncle; swimbladder has short anterior and posterior chambers, the posterior extending to above the pelvic fin (exceptionally, long in *C. minutus,* extending to above the anal fin origin).

Contained species. *Chelaethiops elongatus, C. bibie, C. congicus, C. minutus* and *C. rukwaensis.*

Cranial anatomy

Osteology. The *ethmoid bloc* is short and deep, its anterior border varies interspecifically from shallow to deeply indented (Fig. 3B & C). The lateral edges of the supraethmoid are

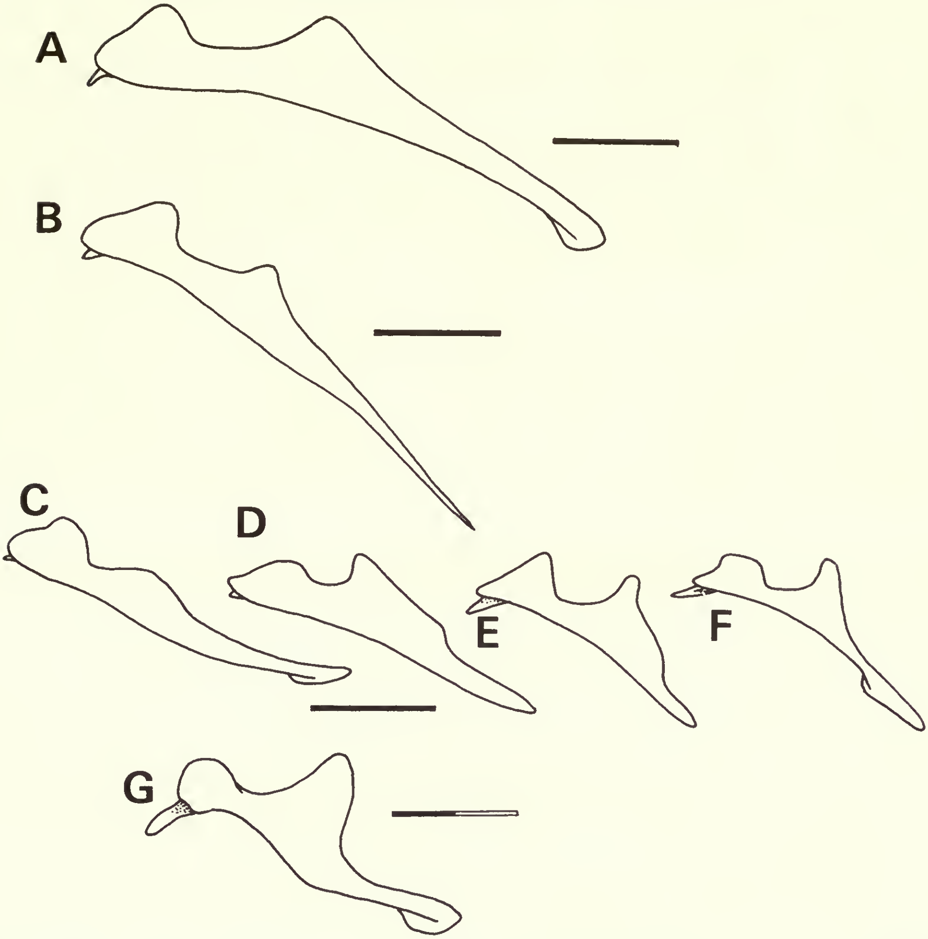

Fig. 7 Maxillae: A, *Neobola bottegi*; B, *Chelaethiops bibie*; C, *Neobola stellae*; D, *Mesobola spinifer;* E, *M. bredoi*; F, *M. brevianalis*; G, *Rasterineobola argentea.* Scales in mm.

raised and the width of the dorsal channel is also interspecifically variable. The mesethmoid is deep, its arms widely divergent, abutting on large preethmoids. The vomer floors the mesethmoidal indentation. As in *Neobola* the lateral ethmoid has an anterior extension of its dorso-lateral wall (lee, Fig. 4).

The *frontals* are narrower than those of other neobolines, the sensory canal is more highly developed, and there are 4 large, conspicuous pores all of which open laterally. The *nasal* is large and reduced to the sensory canal tube with one dorsal pore or none.

The *infraorbitals* more closely resemble those of *Neobola* than any other neoboline genus, both in their width and orbital configuration. The sensory canal, however, runs along the orbital margin of the bones and the 4th infraorbital is longer than in *Neobola* (Fig. 6B).

The *neurocranium* is similar to that of *Neobola* except that the sphenotic has a ventrally directed process, and there is a ventral opening between the basioccipital and the parasphenoid.

The *jaws* are long (Figs 7 & 8); the maxilla has a low, long palatine process and the bone terminates in a spine-like tip. The upper jaw bones are longer and more slender than those of any neoboline genus. The lower jaw closely resembles that of *Neobola* except that the symphysial process of the dentary is more prominent and the coronoid process is lower and backwardly sloped at a shallower angle.

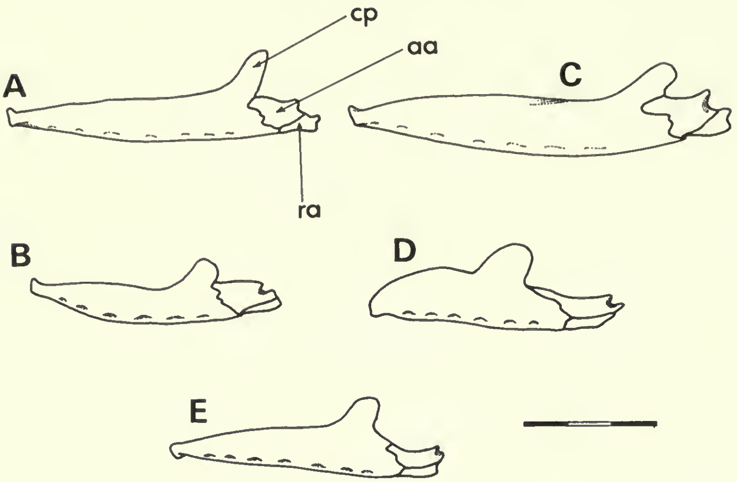

Fig. 8 Lower jaw bones: A, *Neobola bottegi*; B, *Mesobola brevianalis*; C, *Chelaethiops elongatus*; D, *Rastrineobola argentea*; E, *Leptocypris niloticus*. aa = anguloarticular; cp = coronoid process; ra = retroarticular.

The *suspensorial bones* are like those of *Neobola* except that the hyomandibula has a pronounced concavity to its lower anterior border and only a slight indentation separates the articulatory condyles. The posterior condyle is shaped into a long, triangular process. The palatine, ecto-, ento- and metapterygoids are all longer than those elements in *Neobola* and the metapterygoid has only a slight anterior dorsal process (cf. Figs 9A & B).

The *operculum* has a rounded dorsal border and a strongly attentuated, rather triangular lower border (Fig. 9B).

Myology (Fig. 13). Muscle *adductor mandibulae* A_1 is divided into anterior and posterior segments as in *Neobola*. The anterior part A_1*ant*, extends from the quadrate to insert below the maxillary cleft. The segment contains an aponeurotic constriction below the anterior border of the eye. The aponeurosis is divided so that the orbital part serves as the site of the attachment for the fibres from the lower part of the muscle, and the outer division is continuous with the *ligamentum primordium* and serves as the site of attachment for the fibres of the anterior part of that muscle. The posterior segment of muscle A_1, A_1*post*, originates from the preoperculum and inserts on to the coronoid process of the dentary and on the rictal tissue. There is no A_w section of the *adductor mandibulae*. The configuration of other jaw and suspensorial muscles are as described for *Neobola*.

Pectoral girdle (Fig. 10C)

The pectoral girdle resembles that of *Neobola*; the coracoid is deeper than in other neobolines and has a markedly fretted antero-ventral margin. There is no postcleithrum.

Vertebral column (Fig. 12)

The anterior face of the 1st centrum is rounded (*cf.* flat in *Neobola*), the centrum bears long lateral processes, the distal tips of which underlie the processes of the fused 2nd and 3rd centra. The lateral processes of the fused centra are curved posteriorly, their distal tips reaching to a level with the articulation of the 3rd and 4th centra. The neural complex is upright, the 4th neural spine sloped backward at a low angle (Fig. 12). A large plate-like supraneural, possibly two fused supraneurals, overlies the 4th neural spine and extends backwards to above the 5th; this is followed by 6 or more elements varying in shape from triangular plates to thin rods. The caudal skeleton differs from that of *Neobola* in elongation of the 6th hypural, the neural spine on the fused preural-ural centrum and the hypurapophysis (Fig. 17B).

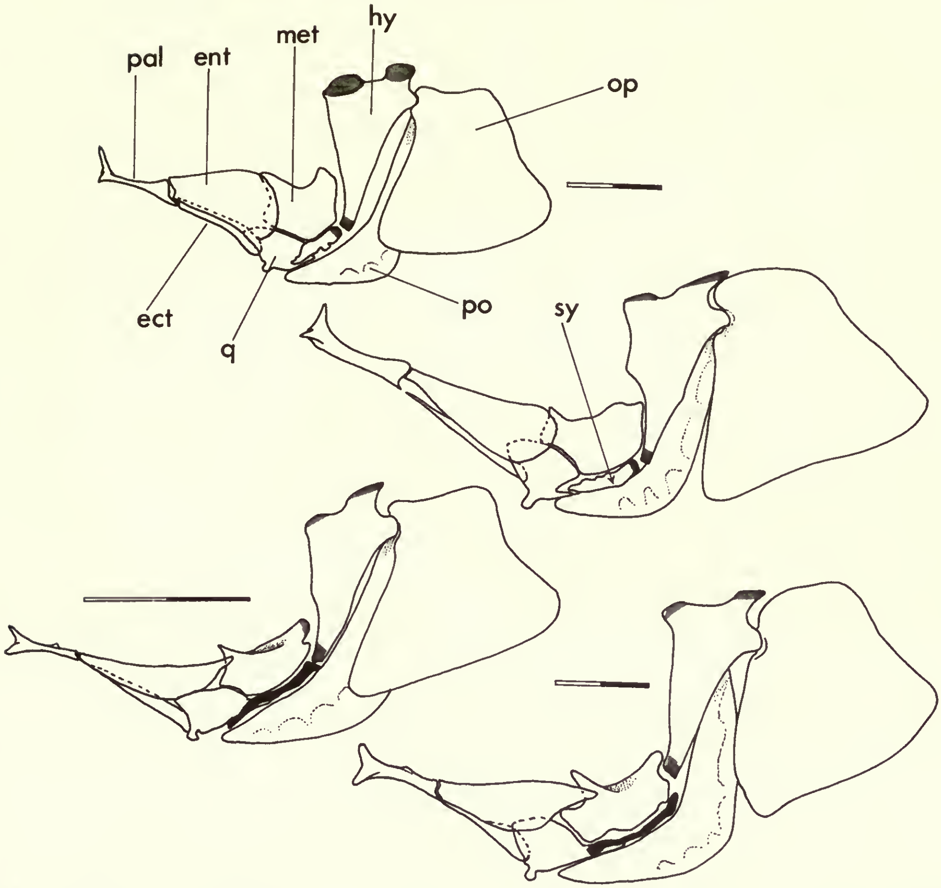

Fig. 9 Suspensoria in medial view: A, *Neobola bottegi;* B, *Chelaethiops elongatus*; C, *Mesobola brevianalis*; D, *Rastrineobola argentea.* ect = ectopterygoid; ent = entopterygoid; hy = hyomandibula; met = metapterygoid; op = operculum; pal = palatine; po = preoperculum; q = quadrate; sy = symplectic. In *Mesobola* and *Rastrineobola,* the symplectic is shown in solid black.

Taxonomy

Boulenger (1911) included two species in *Chelaethiops, viz: elongatus* and *bibie.* Since then only one other species has been described, *C. katangae* Poll, 1948. Howes (1980) assigned three other species to the genus, *Engraulicypris congicus* Nichols & Griscom, 1917, *Neobola minuta* Boulenger, 1906, and *Engraulicypris rukwaensis* Ricardo, 1939.

Chelaethiops elongatus Boulenger, 1899, is characterized by its long and pointed snout and upwardly inclined head (Fig. 19B); a distinct mandibular symphysial notch; 16–17 olfactory lamellae on each half rosette; 5 short gill-rakers on the 1st ceratobranchial; 16–17 branched anal fin rays; 36–38 lateral line scales; axial pectoral scale 30–33% pectoral fin length (Fig. 18C); pectoral fin extending to the origin of the pelvic fin; lower part of posterior opercular border attenuated; pharyngeal teeth in 3 rows, 5.3.2; vertebrae 38 or 39 (4 + 11 – 12 + 21 – 22 + 1, see p. 156 for method of counting). Distribution of the species is the Zaire drainage.

Chelaethiops bibie (Joannis), 1835, is characterized by its narrow supraethmoid with well-developed dorsal channel (Fig. 3C). The snout is pointed but more strongly curved than in *C. elongatus* and there is a prominent ridge above the eye (Fig. 19A). There are 12–13 olfactory lamellae on each half rosette; 9 or 10 short gill-rakers on 1st ceratobranchial; 16–17

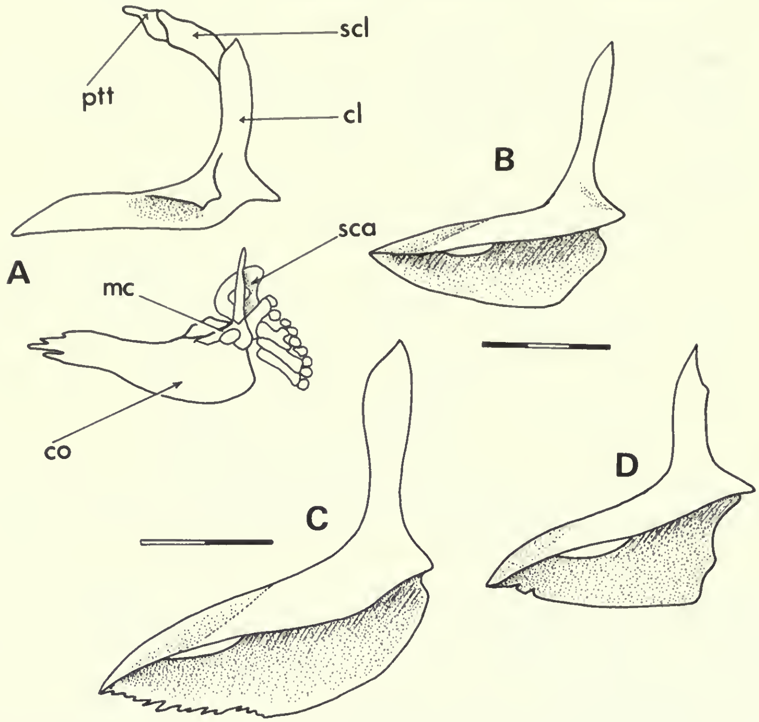

Fig. 10 Pectoral girdles: A, *Neobola bottegi* (medial view of disarticulated girdle); B, *Mesobola brevianalis;* C, *Chelaethiops elongatus*; D, *Rastrineobola argentea* (medial views). cl = cleithrum; co = coracoid; mc = mesocoracoid; sca = scaphium; scl = supracleithrum; ptt = posttemporal.

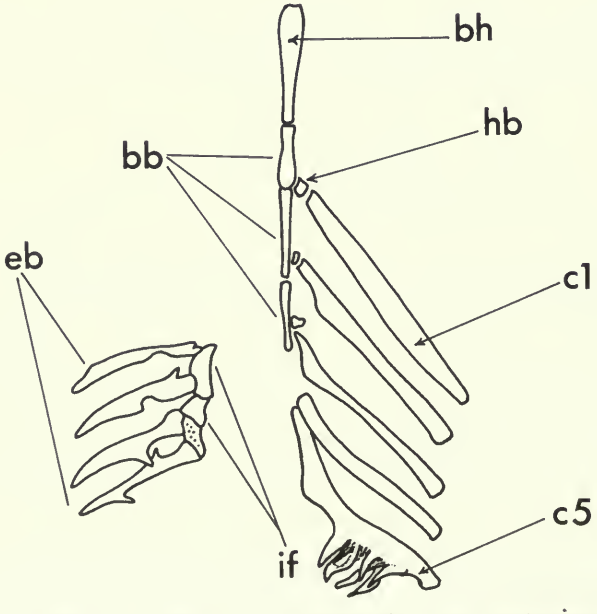

Fig. 11 Branchial arches of *Mesobola brevianalis.* bb = basibranchials; bh – basihyal; C1 – 5 = ceratobranchials; eb = epibranchials; hb = hypobranchials; if = infrapharyngobranchials.

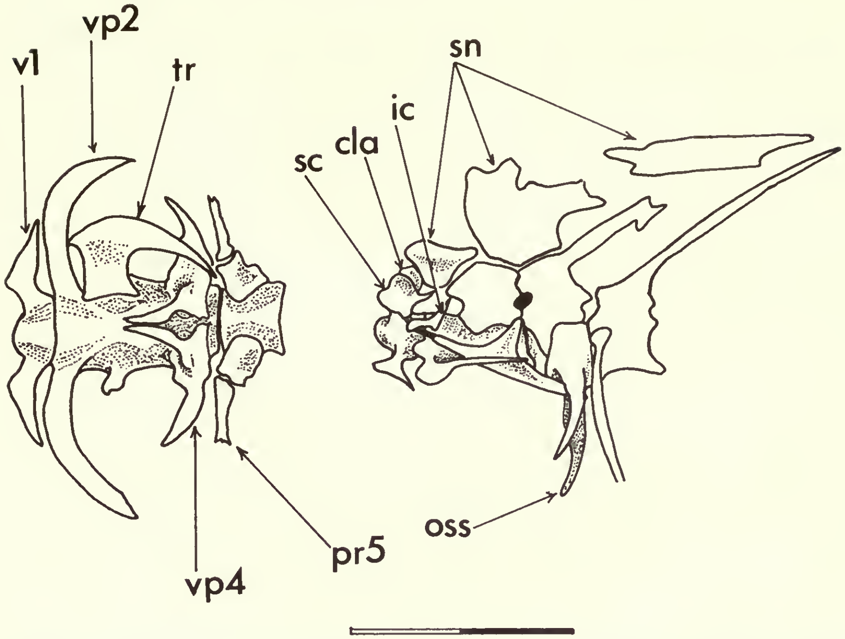

Fig. 12 Anterior vertebrae, in ventral and lateral views, of *Chelaethiops bibie*. cla = claustrum; ic = intercalarium; oss = ossa suspensorium; pr = pleural rib; sc = scaphium; sn = supraneurals; tr = tripus; v = vertebrae; vp = lateral vertebral process.

branched anal fin rays (rarely 14 or 18); 36–38 lateral line scales; the lateral line usually more irregular and sinuous than that of *C. elongatus*; axial pectoral scale about 20% of pectoral fin length (Fig. 18E); pectoral fin extending to beyond the origin of the pelvic fin; lower part of the posterior opercular border attenuated; pharyngeal teeth in three rows, variants are 5.3.1. or 4.3.1; vertebrae 36–40 $(4+11-13+19-22+1)$.

Daget (1954) described a subspecies from the Upper Niger which he named as *C. elongatus brevianalis*. Blache & Miton (1960) decided that Daget's taxon represented a species, which comprised two subspecies, *C.b. brevianalis* and *C.b. lerei* from the Mayo Kebbi. It would seem, however, that Daget did not consider *C. bibie* as he makes no mention of the species in his description. There is no difference between *C. bibie* and Daget's description of *C. elongatus brevianalis*. It may well be that Blache & Miton's (1960) taxon from the Mayo Kebbi represents a subspecies, or morphologically distinct population, but this fact has yet to be established. There are differences in vertebral counts between Nilotic *C. bibie* and those from Ghana as follow: Nilotic specimens; 12 or 13 abdominal and 22 caudal, Ghanian specimens; 11 or 12 abdominal and 19 or 20 caudal. *Chelaethiops bibie* occurs in the Nile (including Lake Turkana), Niger (eastern limit uncertain) and Volta.

Chelaethiops minutus (Boulenger), 1906, is characterized by its narrow supraethmoid with well-developed dorsal channel; long and downwardly curved snout, its tip extending beyond that of the lower jaw (Fig. 19E); a prominent frontal ridge above the orbit; 25–27 olfactory lamellae on each half rosette; 17 or 18 long gill-rakers on the 1st ceratobranchial; 18–21 branched anal fin rays; 39–42 lateral line scales; axial pectoral scale 22–25% pectoral fin length (Fig. 18G); pectoral fin not reaching beyond the origin of the pelvic fin; posterior border of the operculum rounded; pharyngeal teeth in 3 rows, 5.3.2; vertebrae 39 or 40 $(4+12-13+22-23+1)$.

This species differs from other *Chelaethiops* in gill-raker length and number, an elongate posterior chamber of the swimbladder extending to, or just beyond, the anal fin origin and

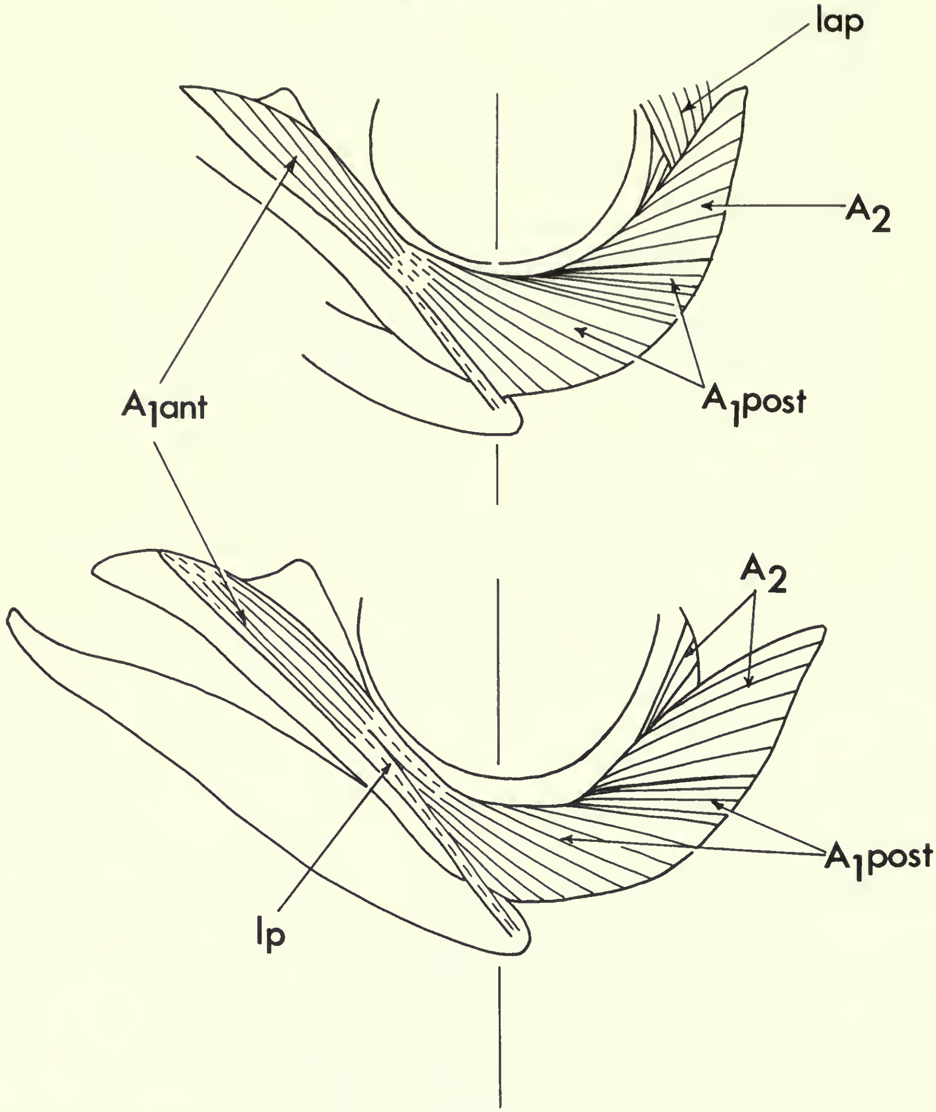

Fig. 13 Jaw muscles of (above) *Neobola bottegi* and (below) *Chelaethiops elongatus.* A = divisions of the *adductor mandibulae* muscle; lp = ligamentum primordium; lap = *levator arcus palatini*; the vertical line marks the orbital centre.

the articulation of the anterior 3 or 4 supraneural bones. It is endemic to Lake Tanganyika (see Poll, 1953).

Chelaethiops congicus (Nichols & Griscom), 1917, is characterized by its short and blunt snout (Fig. 19C); broad supraethmoid with shallow dorsal channel; 12–15 olfactory lamellae in each half rosette; 5–6 short gill-rakers on the 1st ceratobranchial; 16–18 branched anal fin rays; 38–42 lateral line scales; axial pectoral scale 30–33% pectoral fin length (Fig. 18F); pectoral fin extending to the origin of the pelvic fin; upper part of posterior opercular border concave; pharyngeal teeth in 3 rows, 5.4.1 or 5.3.1; vertebrae 41 (4 + 14 + 22 + 1).

It appears that although authors have cited *C. congicus* in their comparative analyses, none has actually examined the type specimens (Poll, 1945; Whitehead, 1962; Ricardo,

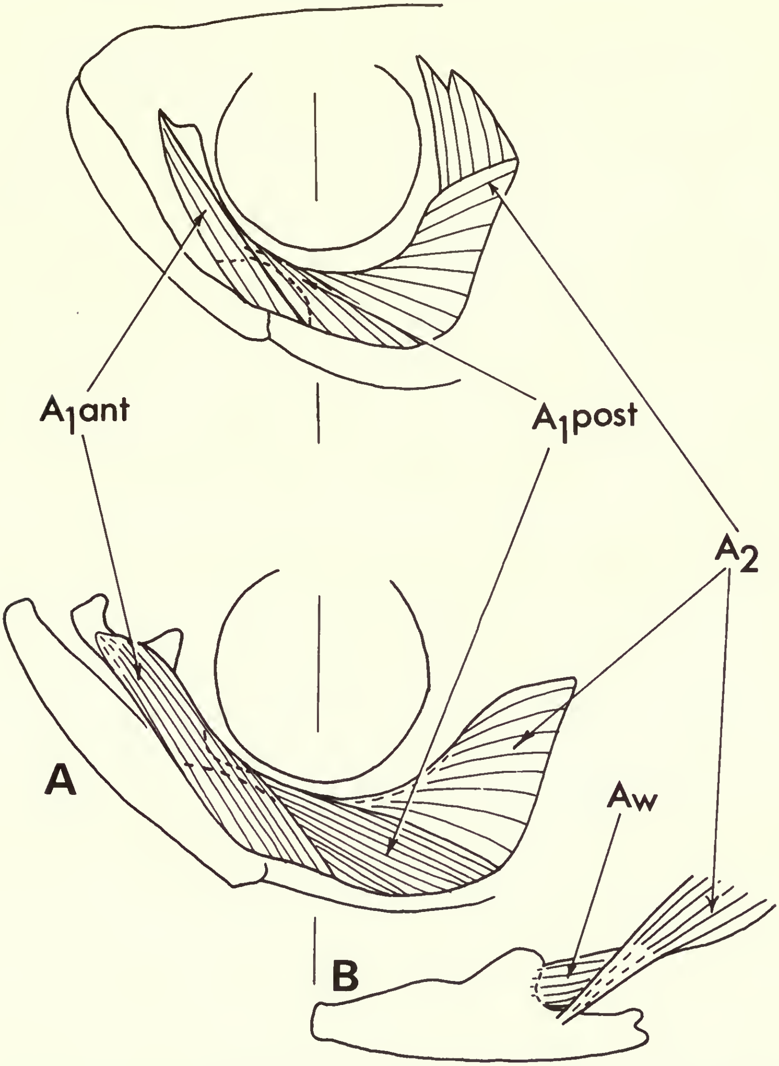

Fig. 14 Jaw muscles of (above) *Mesobola brevianalis* and (below) *Rastrineobola argentea*. A, lateral and B, medial views.

1939). Poll (1948) described *Chelaethiops katangae* from the Lufira, Zaire. Poll did not, however, compare his specimens with *C. congicus* but only with *C. elongatus* and *C. bibie*. I find the holotype of *C. congicus* to be closely similar to the syntypes of *C. katangae* in all morphological aspects and consider *C. katangae* to be a synonym of *C. congicus*. The distribution of *C. congicus* is the Zaire basin.

Chelaethiops rukwaensis (Ricardo), 1939, is characterized by its narrow supraethmoid with well-developed dorsal channel; pointed and curved snout (Fig. 19D); 16–17 olfactory lamellae in each half rosette; 5–6 short gill-rakers on the 1st ceratobranchial; 15–17 branched anal fin rays; 36–38 lateral scales; axial pectoral scale with wavy border (Fig. 18F), 20–25% pectoral fin length; pectoral fin extending to the origin of the pelvic fin; upper posterior border of the operculum shallowly concave, lower border slightly attenuated; pharyngeal teeth in 3 rows, 5.3.1; vertebrae 38–40 (4 + 14 – 16 + 19 + 1).

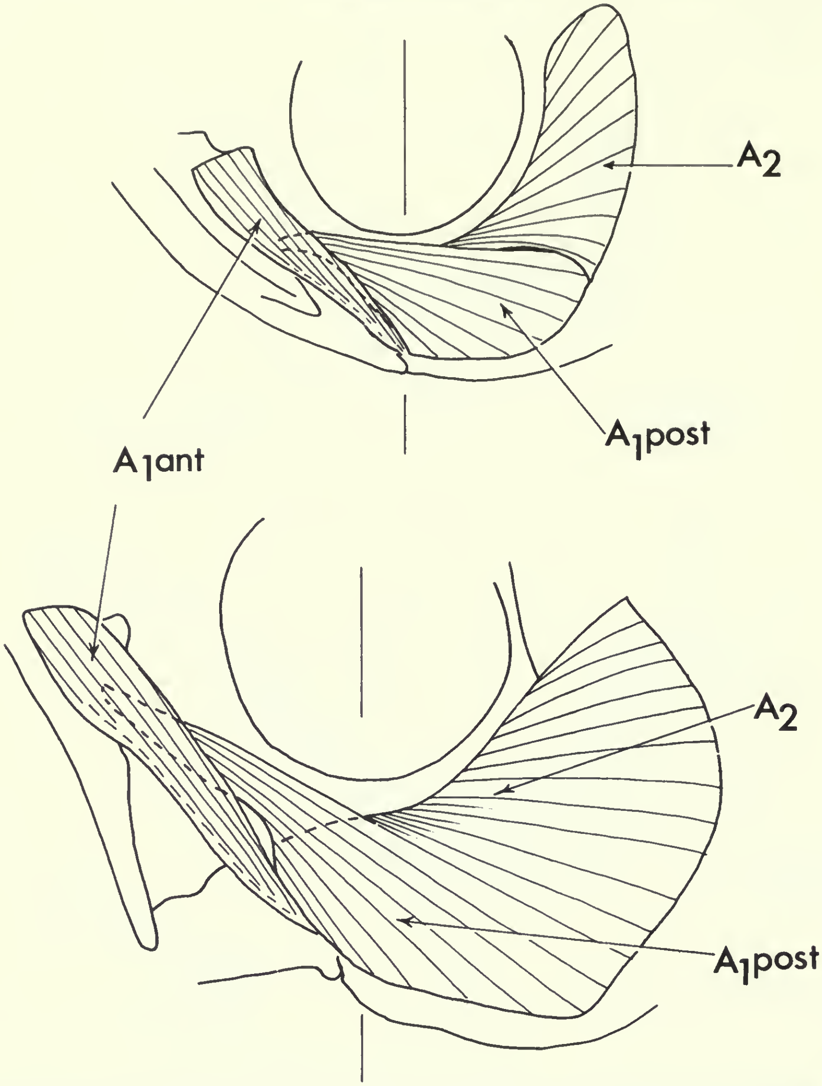

Fig. 15 Jaw muscles of (above) *Leptocypris niloticus* and (below) *Raiamas senegalensis.*

Ricardo (1939) described, from Lake Rukwa, a subspecies of *Chelaethiops congicus*, commenting: 'It is . . . thought best to regard the examples from L. Rukwa as a new subspecies of *E. congicus* in order to show that they do differ from all forms previously known and that they are more closely related to the *Engraulicypris* in L. Tanganyika and the Congo than to any of the species found in other lakes or rivers.'

From this statement it would seem that Ricardo was regarding the subspecies as a convenience category to demonstrate her opinion of relationship. The comparative material from Lake Tanganyika and the Congo used by Ricardo is in fact composite. The specimens from the Congo are those included herein under *C. congicus,* but those from Lake Tanganyika differ in morphometric and other characters and, in these respects, are closer to the samples from Lake Rukwa. As with the Lake Rukwa specimens, the Lake Tanganyika sample has a pectoral axial scale length of 20–25% the pectoral length, *cf.* 30–33% in *C.*

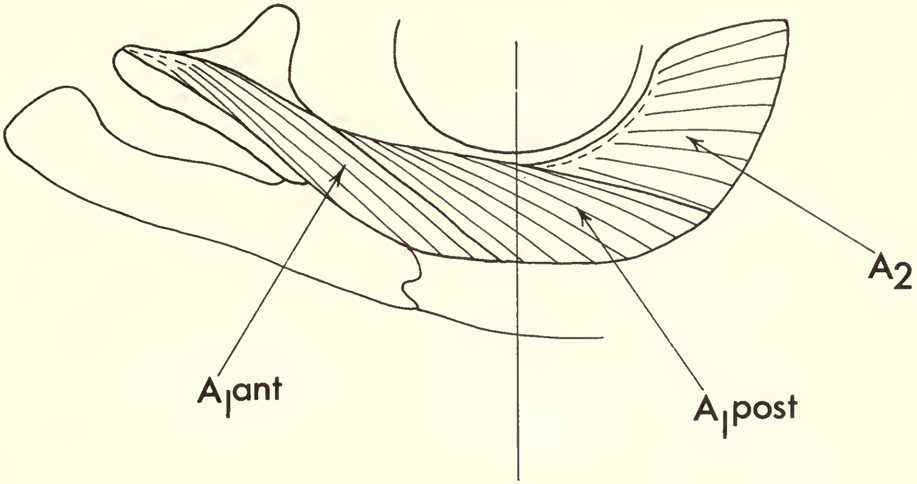

Fig. 16 Jaw muscles of *Engraulicypris sardella.*

congicus, 16–18 olfactory lamellae, *cf.* 12–15 in *C. congicus*, and 36–38 lateral line scales, cf. 38–42 in *C. congicus.*

There is an added difficulty concerning the exact provenance of the 'Lake Tanganyika' sample of *C. rukwaensis.* Neither Poll (1953) nor Brichard (1978) in their respective accounts of Lake Tanganyika fishes record any species of *Chelaethiops* (their *Engrauclicypris*) other than *C. minutus.* The record of Lake Tanganyika *C. congicus* given by Ricardo (1939) is based on the material collected by Christy. No more precise locality is available than 'L. Tanganyika' and it may well be that the specimens were collected in the environs of the lake.

Howes (1980) noted that *C. rukwaensis* was most closely related to an undescribed taxon from Lake Tanganyika. The taxon is the 'L. Tanganyika' sample discussed above. The status of the taxon is difficult to determine on the basis of such a small sample (55 specimens) and with imprecise locality data. It is further complicated by specimens from the Luiche river, Malagarasi system, having characters intermediate between the *C. rukwaensis* and *C. congicus* (*viz:* 38 lateral line scales, 14 branched anal fin rays and 12 olfactory lamellae on each half rosette). The 'L. Tanganyika'-Malagarasi forms may eventually prove to be a morphologically distinct local population (or subspecies) but for the present my study material is identified only as '*Chelaethiops rukwaensis*'.

SPECIMENS EXAMINED. *Chelaethiops elongatus:* 1901.12.26:31, Banzyville Ubanghi; 1912.12.6:9–10, Dungu, Uelle; 1919.9.10.241–2, Avakubi, Ituri; 1920.7.12:39–40, Banghi; 1975.6.20:308–40. 34–43, 344–47, Lualaba; 348–49, Ituri Bridge; MRAC 85848–947, Ankoro, Lualaba.

Chelaethiops bibie. **Nile**: 1904.9.26:22–23. Kalioub, north of Cairo; 1907.13.2:1513–9, near Luxor; 1520–23, between Luxor and Asswan; 1524, Asswan; 1525, Kermeh, Nubia; 1526–1626. Omdurman; 1627, White Nile; 1628–31, Lake No; 1632–51, 52–53, Gondokoro; 1913.11.11:5–7; Khor Barboy; 1924.5.21:1–5, near Cairo; 1981.2.17:1314–1358. Todenyang, L. Turkana; 1369–1431, Morago R., Turkana; 2378–2427, west shore, L. Turkana; 2428–2437, Ferguson's Gulf, L. Turkana. **West Africa:** 1935.5.29:9–18, Kaduna, Nigeria; 1969.11.14:109–23, Volta, Ghana; 1974.1.2:185, Black Volta; 1982.4.13:783–93, Bahindi, Nigeria; 794–797, Sokoto R., 821–830, Sokoto-Rima floodplain; 799–811, 812–820, Rima R., N. Nigeria.

Chelaethiops minutus: 1906.9.8:55–60 (syntypes), Mbete (14–24 mm SL); 1955.12.20:1021–1029, L. Tanganyika (54–66 mm SL); 1982.9.24:61–66, Kigoma (67·5–86·5 mm SL).

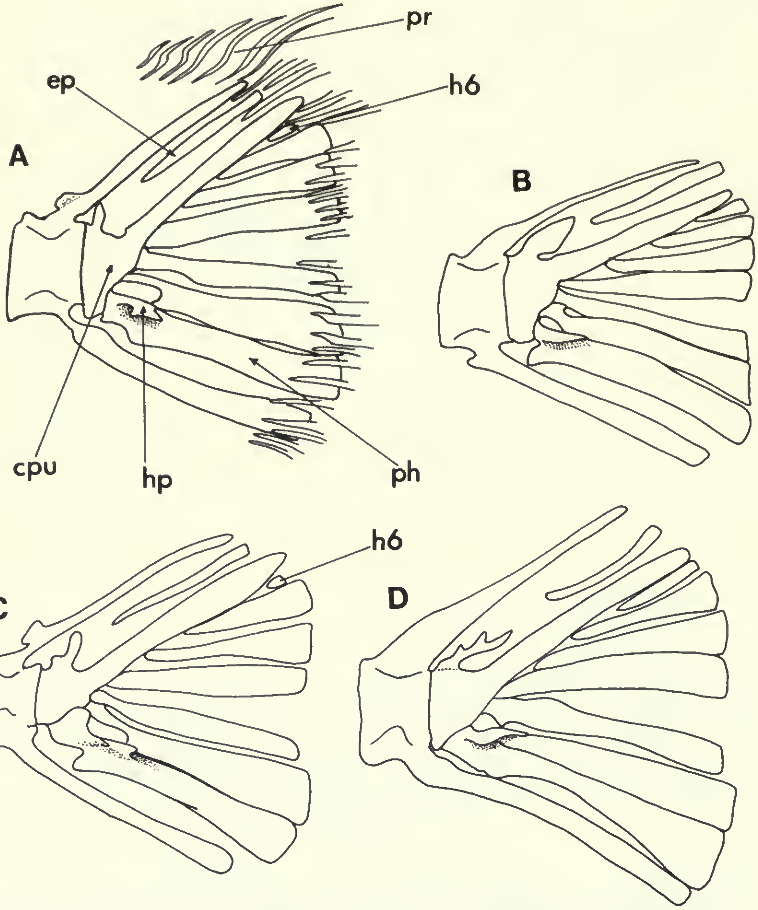

Fig. 17 Caudal fin skeletons: A, *Neobola bottegi*; B, *Chelaethiops elongatus;* C, *Mesobola brevianalis;* D, *Rastrineobola argentea.* cpu = fused preural-ural centrum; ep = epural; h6 = 6th hypural; hp = hypurapophysis; ph = parhypural; pr = procurrent rays.

Chelaethiops congicus; AMNH 6295 (holotype), Poko, Ubangi; MRAC 78108–9 (syntypes of *C. katangae*), Kafila, Lufira; BMNH 1919.9.10:238, Avakubi, Ituri; 1919.9.10:239, Busabangi, Lindi; 1902.4.14:47–8, Lindi R.; 1907.4.30:42, Atuwimi R.; 1909.7.9:62, Bumba (Boumba) R., Assobam, S. Cameroon; 1975.6.20:350–402, Lufira R.
Chelaethiops rukwaensis; 1942.12.31.:191–210 (syntypes), Lake Rukwa; 1936.6.15:547–67, 'L. Tanganyika'; 1969.1.31:49–105, Lake Rukwa; 1971.6.22:137–138, Luiche R., Malagarasi system.

MESOBOLA gen. nov.

TYPE SPECIES. *Engraulicypris brevianalis* Boulenger, 1908, *Ann. Natal Mus.* **1**: 231

This genus is uniquely defined by its cranial, jaw bone and jaw muscle morphology. At the same time it can be included with *Neobola, Chelaethiops* and *Rastrineobola* on the basis of those synapomorphies defining the neoboline group (p. 177). *Mesobola* is characterized by a narrow, dorsally channelled supraethmoid; vomer forming a floor to the ethmoid indentation; pre-ethmoids directed rostrad; nasal without dorsal pores; frontal canal with 4 or 5 pores; narrow, triangular metapterygoid process; symplectic elongate with expanded tips;

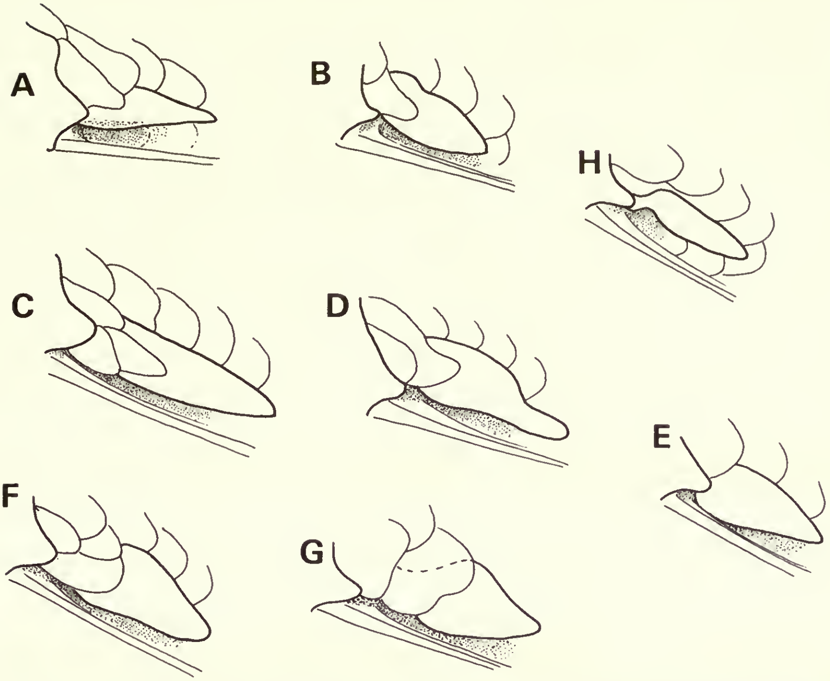

Fig. 18 Pectoral axial scales: A, *Neobola bottegi*; B, *Neobola stellae*; C, *Chelaethiops elongatus*; D, *C. rukwaensis*; E, *C. bibie*; F, *C. congicus*; G, *C. minutus.*

8–10 olfactory lamellae on each half rosette; pectoral axial scale absent; pharyngeal teeth in 3 rows; swimbladder with long anterior and posterior chambers, the posterior curved downward and terminating above the anus.

CONTAINED SPECIES. *M. brevianalis, M. spinifer, M. bredoi* and *M. moeruensis.*

Cranial anatomy

Osteology. The most characteristic feature of the cranium is the morphology of the ethmoid region (Fig. 3D). The *ethmoid bloc* is hour-glass shaped, the supraethmoid with a deep anterior notch, its lateral walls lamellate and forming a deep channel posterior to the notch. The mesethmoid has a V-shaped anterior indentation, the preethmoids being situated on the tips of the mesethmoid arms and thus considerably extending the depth of the indentation. The vomer floors the notch and where it meets the preethmoids there is a thickening of the bone, thus forming what appears to be medial processes of the preethmoids. In some specimens there is a small vomerine foramen. The lateral ethmoid margin curves antero-ventrally and lacks the dorsal lamellae present in *Neobola* and *Chelaethiops.*

The frontal canal (Fig. 2C) lies close to the edge of that bone and has 4–5 pores. The size and position of the canal pores is interspecifically variable, but the posterior pore always opens laterally. The *nasal* is large, lacking dorsal pores. The *cranial roof* is convex in the area of the fronto-parietal suture; in all other neoboline genera the roof is flat.

The *infraorbitals* (Fig. 6C) are shallow, as in *Rastrineobola* (*cf.* deep in *Neobola* and *Chelaethiops*). The infraorbital canal runs along the ventral part of the 1st bone, the orbital border of the 2nd and through the centres of the 3rd, 4th and 5th infraorbitals.

The *orbitosphenoids* are connected to the parasphenoid *via* a deep, narrow septum. The anterior trigemino-facialis foramen indents the border of the *prootic* and there is a long lateral commissure (Fig. 5). There is a small foramen between the parasphenoid and basioccipital.

The *jaws* are long (Figs 7 & 8); the palatine process of the maxilla varies interspecifically from being low and long, to high and triangular in shape (see p. 180 & Figs 7D–F). The articulation of the dentary with the quadrate is below the centre of the orbit. The dentary is rather deep with a convex dorsal border and a backwardly sloped coronoid process. The anguloarticular has a long, almost horizontal dorsal border.

The *suspensorium* (Fig. 9C). The hyomandibula is narrow with a straight anterior border. The dorsal border is sloped so that the anterior articulatory condyle is at a level lower than that of the posterior condyle. The ento- and metapterygoids are deeper than those of other genera. The entopterygoid is long with a slightly concave dorsal border; the metapterygoid has a narrow, triangular anterior process directed mesad. The most noticeable feature of the suspensorial elements is the length and shape of the symplectic. The bone is excessively elongate with expanded tips where it contacts the quadrate and the hyomandibula.

Branchial arches (Fig. 11). The ceratobranchials bear 7–12 long gill-rakers, pharyngeal teeth are arranged in 3 rows with interspecific variation of 4.2.1, 4.3.1 and 5.3.2.

The *operculum* has a concave upper posterior border and an attentuated lower part (Fig. 9C).

Myology (Fig. 14). As in *Neobola* and *Chelaethiops,* section A_1 of the *adductor mandibulae* muscle is divided, but A_1*ant* lacks the aponeurotic constriction present in those two genera and extends from the quadrate to insert below the anterior cleft of the maxilla. Muscle A_1 *post* extends from the lower limb of the preoperculum to insert partly on the coronoid process of the dentary and partly, *via* a long tendon, into the fascia of A_1*ant*. Other muscles are arranged as in *Neobola.*

Pectoral girdle (Fig. 10)

The upright part of the cleithrum is narrower than in *Neobola* and more closely resembles that of *Chelaethiops* in shape; the coracoid is deep and its posterior border forms a sharp angle with the ventral border. There is no postcleithrum.

Vertebral column

The 1st vertebra has a flat anterior face, and short, blunt lateral processes. The 2nd and 3rd centra are fused, bearing long, lateral processes with posteriorly curved tips. The caudal fin skeleton closely resembles that of *Neobola* in having a small 6th hypural and reduced spine on the fused ural centrum, and short hypurapophysis (Fig. 17C). There are no paired uroneurals. Dorsal and ventral procurrent rays are well-developed.

Taxonomy

Mesobola brevianalis (Boulenger), 1908, is characterized by a maxilla with a high, narrowly triangular mid-lateral (palatine) ascending process (Fig. 7F); 10 olfactory lamellae on each half rosette; absence of pectoral axial scales; 12–15 branched anal fin rays (12 in the type specimen, 14–15 in others); 9–12 gill-rakers on 1st ceratobranchial; 48–50 lateral line scales, the lateral line with a pronounced and abrupt downward curve over the pectoral fin, and another at the caudal fin base; pectoral fin reaching to origin of the pelvic; pharyngeal teeth in 3 rows, interspecific variation, 4.2.1–5.3.2; swimbladder with long anterior and posterior chambers, the posterior curving downward and terminating above the anus; vertebrae 39 or 40 $(40+13-14+20-22+1)$.

Jubb (1967) gives a description, synonymy and distribution for the species. Bell-Cross (1956*a*) records *M. brevianalis* from the Kabompo river and an 'isolated' example from Fort Rosebery, off the Luapula river. Jubb (1967) refers to *M. brevianalis* from the Cunene river, although this species is not listed by Bell-Cross (1965*b*) in his check-list of the fishes of that river. The species is recorded from Zambia, Zimbabwe, Transvaal and Natal. On the western side of South Africa, it occurs below the Aughrabies Falls of the Orange river (Jubb, 1967 : 127).

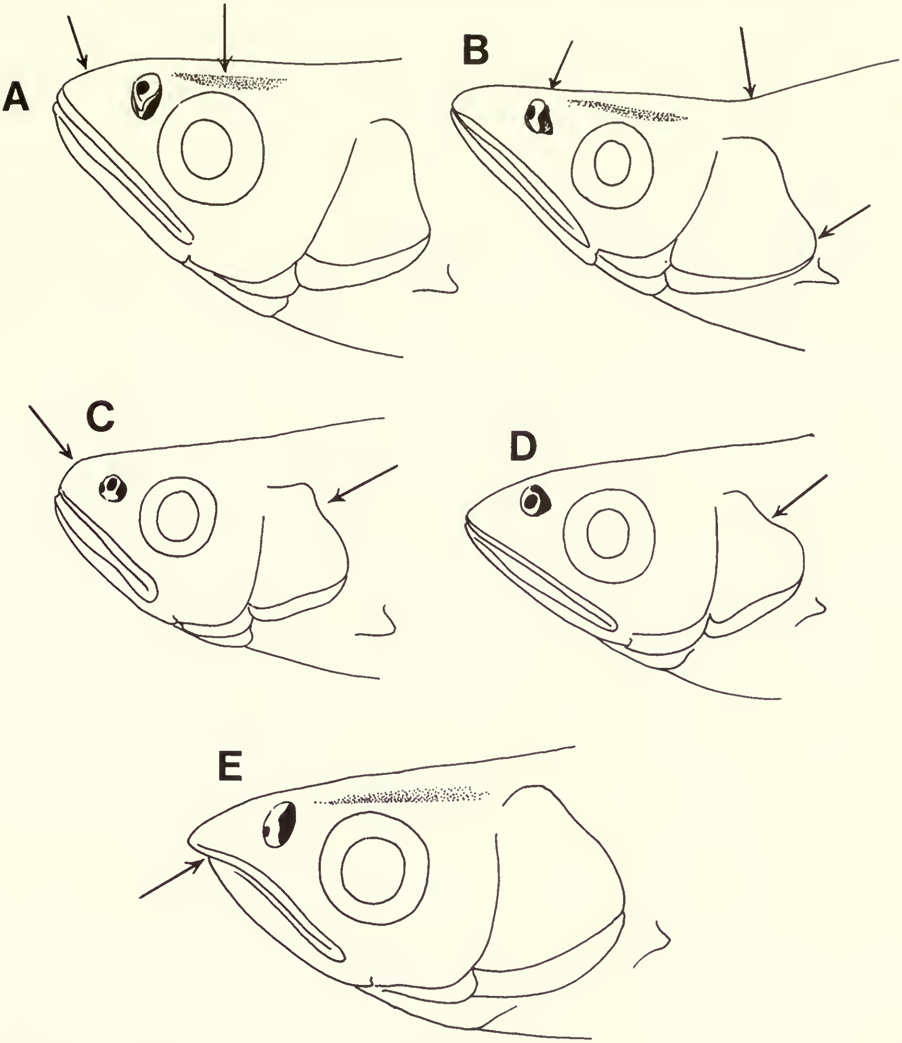

Fig. 19 Characteristics of *Chelaethiops* species: A, *C. bibie*; B, *C. elongatus*; C, *C. congicus*; D, *C. rukwaensis*; E, *C. minutus*. The arrows indicate specific features; length and shape of snout, inclination of head, prominence of frontal ridge, shape of opercular border.

Mesobola bredoi (Poll), 1945, is characterized by a maxilla with a high and narrowly triangular palatine process (Fig. 7E); low number of olfactory lamellae, 8 on each half rosette; 11–13 anal fin rays; lateral line scales 36–39; 12 long gill-rakers; pharyngeal tooth formula: 4.2.1; vertebral number 37–39 ($4+12-13+19-21+1$). The species is confined to Lake Albert.

Mesobola moeruensis (Boulenger), 1915, is characterized by a maxilla with a low, sloped palatine process; 9 long gill-rakers; the lower posterior border of the operculum attenuated; 8 olfactory lamellae on each half rosette; 15 branched anal fin rays; lateral line scales 41; pharyngeal tooth formula, unknown; vertebral number 38 ($4+12+21+1$). All characters taken from a syntype.

A sample of 10 specimens from Katanga (MRAC 85812–847) named as this species, have gill-rakers less spinose than those of the type specimen and more closely resembles *M. spinifer*. *Mesobola moeruensis* is most probably confined to Lake Mweru, and those samples from elsewhere named as this species belong to some other taxon.

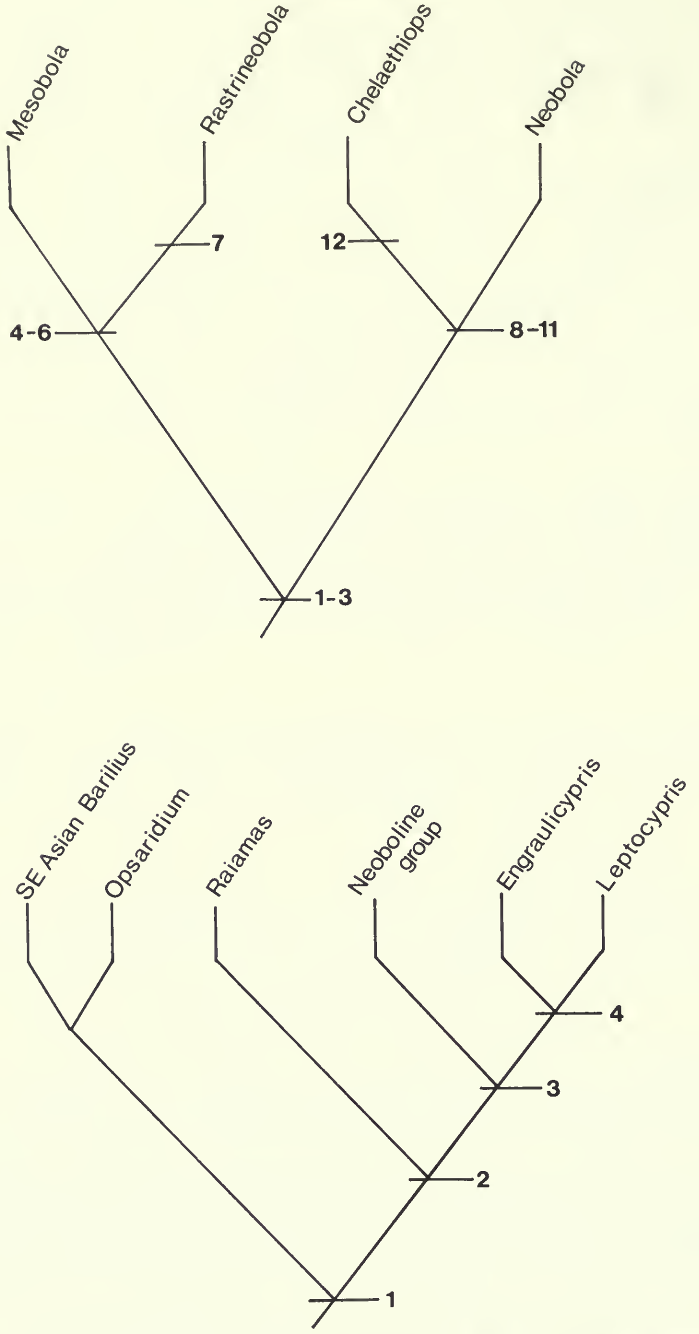

Fig. 20 Above, synapomorphy scheme of the neoboline group. Synapomorphies are, 1, channelled supraethmoid; 2, frontal canals at edge of the bones with extensive, laterally opening pores; 3, divided A_1 muscle with complex aponeurotic inclusions; 4, derived ethmovomerine morphology; 5, elongate symplectic; 6, derived jaw morphology; 7, forward shift of jaw articulation; 8, anterior extension of lateral ethmoid; 9, aponeurotic constriction of muscle A_1*ant*; 10, enlarged frontal pores; 11, hypertrophied supraneurals; 12, divided A_1 aponeurosis (see text, pp. 179). Below, cladogram showing relationships of the neoboline group. Synapomorphies are, 1, divided A_1 muscle; 2, pectoral axial scales (secondarily lost in some taxa); 3, A_1 *post* muscle insertion divided; 4, derived ethmovomerine morphology (see text, pp. 181).

Mesobola spinifer (Bailey & Matthes), 1971, is characterized by a maxilla with a low, sloped palatine process (as in *M. moeruensis*); 7–8 olfactory lamellae on each half rosette; 9–11 gill-rakers on 1st ceratobranchial; 15–16 branched anal fin rays; lateral line scales, 41–45; pharyngeal tooth formula, 4.3.2.; vertebral number 39–41 (4+13+21–23+1).

Bailey & Matthes (1971) compare *M. spinifer* with other species here included in *Neobola* and *Mesobola* and conclude that it is most closely related to *M. moeruensis.* They distinguish *spinifer* from *moeruensis* principally on the higher number of gill-rakers. However, in the syntype of *M. moeruensis* I count 9 rakers on the ceratobranchial, not 7–8 as given by Bailey & Matthes. There is no substantial difference in lateral line scales and branched anal fin ray counts. Bailey & Matthes (1971) also distinguish *M. spinifer* from *M. moeruensis* on body depth. The authors give a body depth range of 18·3–21·8% of SL for *M. spinifer* but give no figures for *M. moeruensis.* The body depth for the only examined syntype is 22·8% of the SL and the range for the Katangan specimens of *'moeruensis'* (see above) is 21·1–24·7% (mean 23·5%). In numbers of branched fin anal fin rays (16–18) and vertebral count (total 39–40), the Katangan specimens of *M. 'moeruensis'* are closer to *M. spinifer* than to the type specimen of *M. moeruensis. Mesobola spinifer* occurs in the Malagarasi and Ruaha drainages (see Bailey & Matthes, 1971).

Specimens examined. *Mesobola brevianalis:* 1907.4.17:90 (holotype), Mkuzi R., Zululand; 1907.5.15:5–7, Devaard R., Transvaal; 1915.6.29:15–17, Aapies R., at Petronella; 1977.6.27:299–300, Namaini Pan, Pongolo R.; 1977.6.27:307–1256, Pongolo R., below Jazini Dam, Mzinyeni Pan, N. Natal; 1982.4.13:4693–97, Sabe R., Chisumbanje, Zimbabwe; 1978.8.3:158–62, L. Chiuta; MRAC 186489–947, Chambesi R., Rhodesia.
Mesobola bredoi: 1969.3.18:1–15, Lake Albert.
Mesobola moeruensis, 1920.5.26:84 (syntype), Lake Mweru; *Mesobola 'moeruensis'* MRAC 85812–847, Elizabethville, Katanga.
Mesobola spinifer: 1970.3.10:1 (holotype), Kazima, Malagarasi watershed; 1970.3.10:2–9; 10–11 (paratypes), same locality as holotype.

RASTRINEOBOLA Fowler, 1936

Rastrineobola argentea (Pellegrin), 1904 is the type and only species of the genus. It is characterized by an elongate ethmoid region, short, deep jaws, long gill-rakers, 10 olfactory lamellae on each half rosette, absence of pectoral axial scale and a swimbladder with long anterior and posterior chambers, the posterior curving downward and extending to above the anus.

Cranial anatomy

Osteology (Figs 2, 3 & 5). The ethmoid bloc is long, narrow and deep. The lateral edges of the supraethmoid are raised forming a shallow dorsal channel; posteriorly the bone is overlapped by the frontals. The mesethmoid has an omega-shaped (Ω) indentation, the lateral arms abut on long, anteriorly directed preethmoids. The vomer floors the mesethmoid indentation and its anterior border is also strongly indented. The exposed portion of the vomer, between the mesethmoid arms, is sometimes perforated (Fig. 3E). The lateral ethmoid has a marked lateral protrusion (*cf.* the truncated condition in *Neobola* and *Chelaethiops*) from the frontal margin and is sloped anteroventrally.

The *frontal canal* in common with other neobolines lies on the margin of the bone and has 3 dorsally directed sensory pores; the 4th pore opens laterally. The *nasal* is broad, lacking dorsal pores.

The morphology of the *neurocranium* is essentially like that of *Mesobola* except in having a flatter cranial surface, smaller sphenotic, straighter edged pterotic, longer basioccipital and parietals. The supraoccipital is also shorter than in *Mesobola* and bears a slight crest (Fig. 5). There is a ventral opening between the basioccipital and parasphenoid.

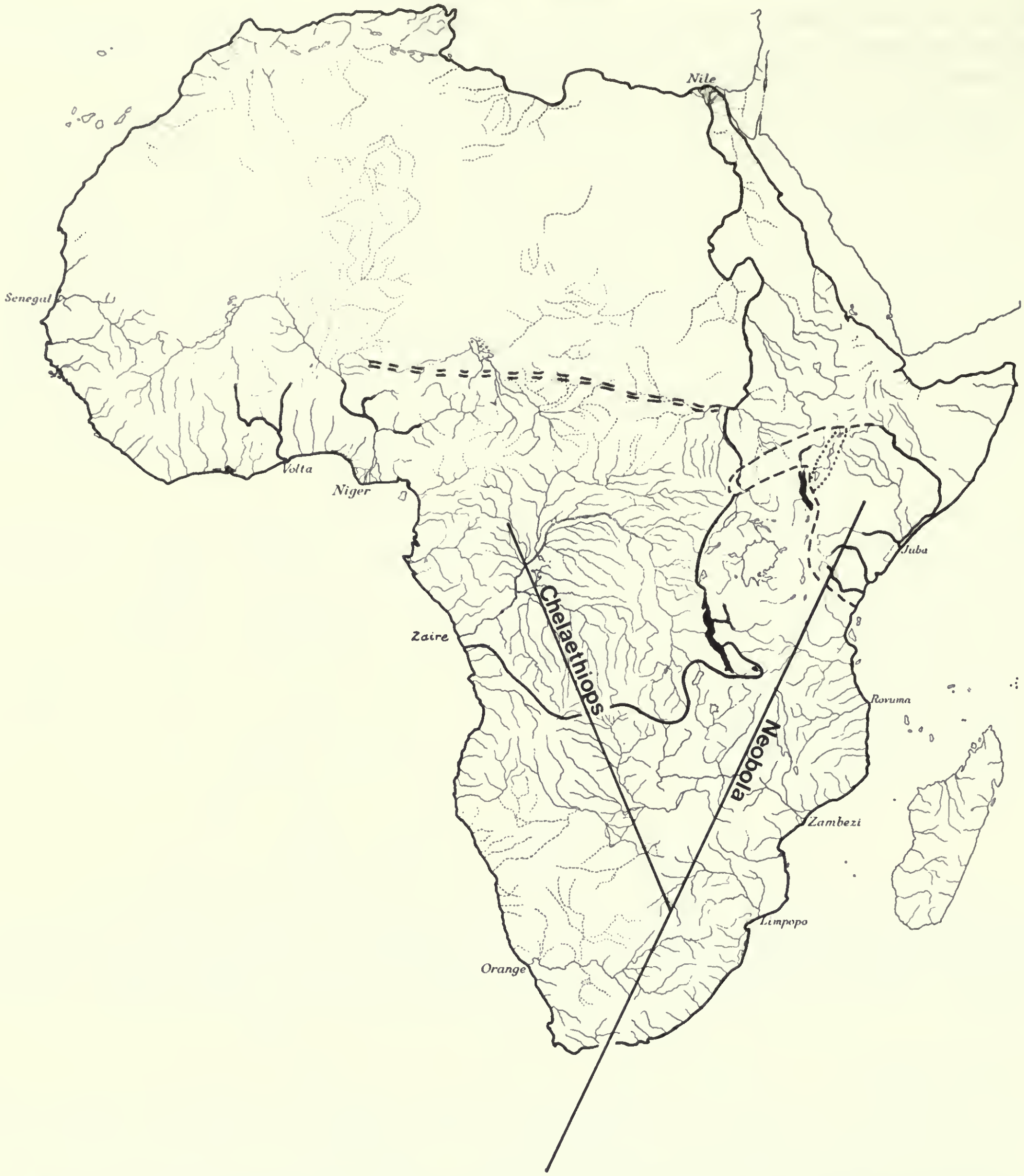

Fig. 21 Distribution of *Neobola* and *Chelaethiops*. The single dashed line indicates the probable limit of *Neobola* distribution; the area enclosed by the dotted line is devoid of any records of *Neobola* species. The Nile marks the eastern boundary of *Chelaethiops*, that in the west is unknown and is indicated as the Volta, the northern extent is marked by a double-dashed line. The lakes where *Chelaethiops* species occur are shown in solid black.

The *infraorbitals* (Fig. 6D) are all of approximately the same depth, the 1st is broadly triangular with the sensory canal passing through its centre, the 2nd bears an antero-dorsal process and the canal, as in the 3rd, 4th and 5th, runs through the centre of the bone. The 5th infraorbital is separated from the wide supraorbital.

The *jaws* (Figs 7 & 8) are shorter than in other neobolines. The maxilla bears a high mid-lateral (palatine) ascending process with a convex (*cf.* concave) posterior border (Fig. 7G).

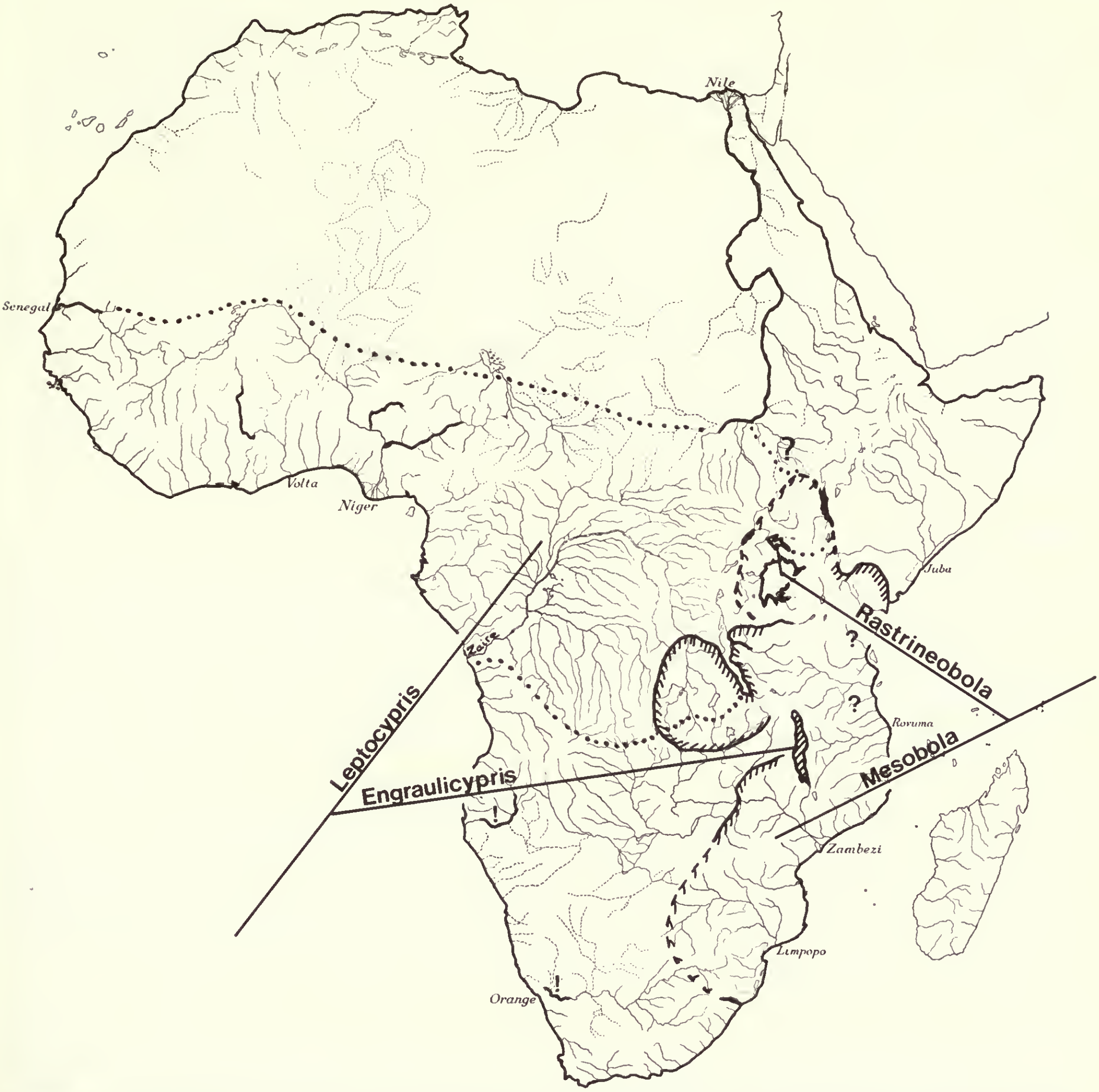

Fig. 22 Distribution of *Mesobola, Rastrineobola, Leptocypris* and *Engraulicypris*. The supposed limits of *Mesobola* species are indicated by hatched lines, the lakes where they occur by solid black. Exclamation signs mark the western records. The Nile is the eastern boundary of *Leptocypris*, while the dotted lines indicate the supposed northern and southern boundaries. *Rastrineobola* occurs only in Lakes Victoria and Kioga, and *Engraulicypris* in Lake Malawi.

Anteriorly the maxilla is not bifurcated as in the other genera where the arms of the bifurcation are of equal length. Instead the medial arm is the longer and is directed ventrally. The ventral border of the maxilla is concave. The premaxilla has a short anterior ascending process. The dentary is deep with a convex dorsal border and a high, rounded coronoid process, halfway along the bone. The anguloarticular is long with a horizontal dorsal surface (Fig. 8D).

Suspensorium (Fig. 9D). The hyomandibula is broadly triangular, its anterior edge vertical; the articulatory condyles are widely separated, the intervening border of the bone being gently concave. The metapterygoid bears a well-developed, narrow process which is directed medially and overlies the posterior margin of the entopterygoid. The ectopterygoid is a short, deep bone (*cf.* long and slender in other neobolines). As in *Mesobola*, the symplectic is elongate with expanded tips and extends the length of the metapterygoid.

Branchial arches. The ceratobranchials are short with 12 or 13 long gill-rakers; epibranchials with 3 or 4; pharyngeal teeth long and recurved, in 3 rows, 4.3.2. Infrapharyngobranchial 2 is short and almost square, compared with a longer, triangular element in other neobolines.

The *operculum* (Fig. 9D) is long with a sloped and rounded posterior border.

Myology (Fig. 14). As in *Mesobola,* the *adductor mandibulae* section A_1 is divided, the anterior part, A_1*ant*, originating from the quadrate and inserting musculosly on to the anterior part of the maxilla; the posterior part, A_1*post*, originates from the preoperculum to insert in part *via* a long tendon into the medial fascia of A_1 *ant* and in part on to the dorsal rim of the coronoid process of the dentary.

Muscle A_2 originates from preoperculum and is divided by the *levator arcus palatini.* The muscle inserts *via* a long tendon on to the medial face of the anguloarticular; a small segment of muscle runs from the tendon of A_2 to the medial rim of the coronoid process, this segment is taken to represent A_w (Fig. 14B).

Pectoral girdle (Fig. 10D)

The upright part of the cleithrum is short, the tip of the horizontal limb extending to a point below the parasphenoid ascending process. There is a longer upright cleithral lamina than in other neobolines. The coracoid is deeper posteriorly than in any other neoboline and has an irregularly shaped posterior border; there is also a slight fretting of the anteroventral margin in some specimens.

Vertebral column

The 1st centrum has a flat articulatory face and long lateral processes; the 2nd and 3rd centra are fused with long, recurved lateral processes. There are 38–40 vertebrae (4 + 16 + 17 + 19 + 1). The caudal skeleton (Fig. 17D) more closely resembles that of *Chelaethiops* in having a long 6th hypural; it differs from other neobolines in possessing a bifurcate or trifurcate spine on the fused ural centrum, a bowed epural and anteriorly expanded neural spine on the 1st preural centrum. There is a long hypurapophysis.

Taxonomy

There is a considerable variation in lateral line scale counts in the several samples examined. Also, there is a higher range of branched anal fin rays in a sample from Lake Kioga than in those from Lake Victoria. The compared samples are, however, small and it is possible that there may be a greater overlap of minimum values than those indicated:

Locality	N	SL range (mm)	Scales in LL.	Mean	Anal rays
Mwanza	51	49·0–70·0	42–56	50	12–14
Entebbe	20	38·5–78·7	44–56	49	12–14
Lake Kioga	13	38·0–52·6	40–54	49	14–16

In the sample from Entebbe the largest specimen examined, 78·7 mm SL, has 51 scales compared with 56 in a specimen 52·5 mm SL.

Specimens examined. *L. Victoria:* 1905.2.28:2–8 (syntypes), Kavirondo Bay; 1906.5.30:146–51, Bunjako; 1908.10.19:8, Sesse Island; 1909.7.27:11, Kavirondo Bay; 1909.11.15:20, Kizumu Bay; 1964.2.20:12–18, Entebbe; 1982.9.24:1–10; 41–50, Entebbe; 1982.9.24:31–40, Katebo; 1982.9.24:11–20, Mwanza; 50 specimens measured at Mwanza but not preserved. *Lake Kioga:* 1929.4.16:21–22; 1939.3.8:1–10; 1982.9.24:21–30; 1982.9.24:51–60.

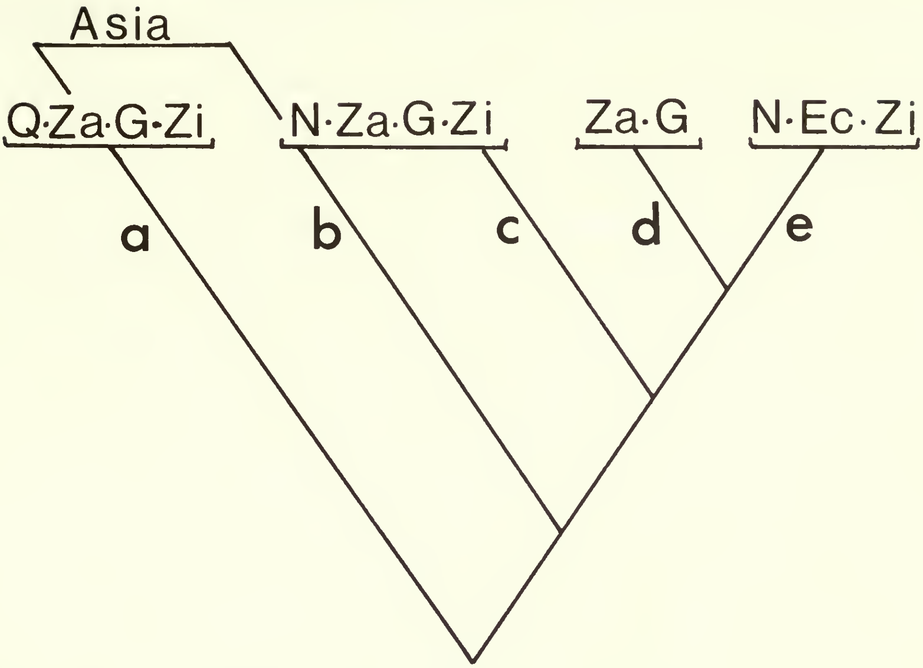

Fig. 23 Reduced area cladogram of African bariliines and neobolines. a = *Opsaridium* + Asian bariliines; b = *Raiamas*; c = *Leptocypris* + *Engraulicypris*; d = *Chelaethiops*; e = other neoboline genera. EC = East Coast; G = Guinean; N = Nilo – Sudanian; Q = Quanzan; Za = Zairean; Zi = Zambesian.

Phylogenetic relationships of the neoboline group

Monophyly

The assumed monophyly of *Neobola, Chelathiops, Mesobola* and *Rastrineobola* is based on the following synapomorphies:

1. *Ethmovomerine morphology.* The supraethmoid in all neobolines is narrow and dorsally channelled (see p. 152). The plesiomorphic cyprinid supraethmoid is broad and flat (see Howes, 1981).

Within the neobolines, the most extreme form of supraethmoid channelling occurs in *Mesobola* (Fig. 3D). The width and development of the dorsal channel varies interspecifically in *Chelaethiops* (Figs 3B & C). In *Neobola* the dorsal channel is least developed.

Howes (1979) argues that the overlap of the supraethmoid by the frontals is a synapomorphy for chelines and possibly *Chelaethiops* (*Engraulicypris* of Howes, 1979). However, further study shows a similar condition in several other cyprinid taxa, usually in juveniles, where it is an ontogenetic precursor to the sutured joint of the adult. Where it survives in adults, it must be looked upon as ontogenetic retention and therefore plesiomorphic.

2. *The frontal canals situated at the edge of the bone.* Frontal canals occupy the border of the bone only in neobolines. The sensory canal openings are few (3–5), of large aperture, and in *Neobola* and *Chelaethiops* alone all open laterally (Fig. 2).

The common condition in cyprinids is for the frontal sensory canals to be embedded within the bone, distant from its margin and with small dorsal pores. See Howes, 1981 : 17–18 for an account of the plesiomorphic cyprinid frontal.

3. *A derived jaw muscle morphology.* In all neobolines, the *adductor mandibulae* A_1 section is divided into anterior (A_1*ant*) and posterior (A_1*post*) segments. A_1*ant* originates from the quadrate and inserts on the maxilla; A_1*post* originates from the lower part of the preoperculum and inserts variously into the lower jaw bone and rictal tissue (see below).

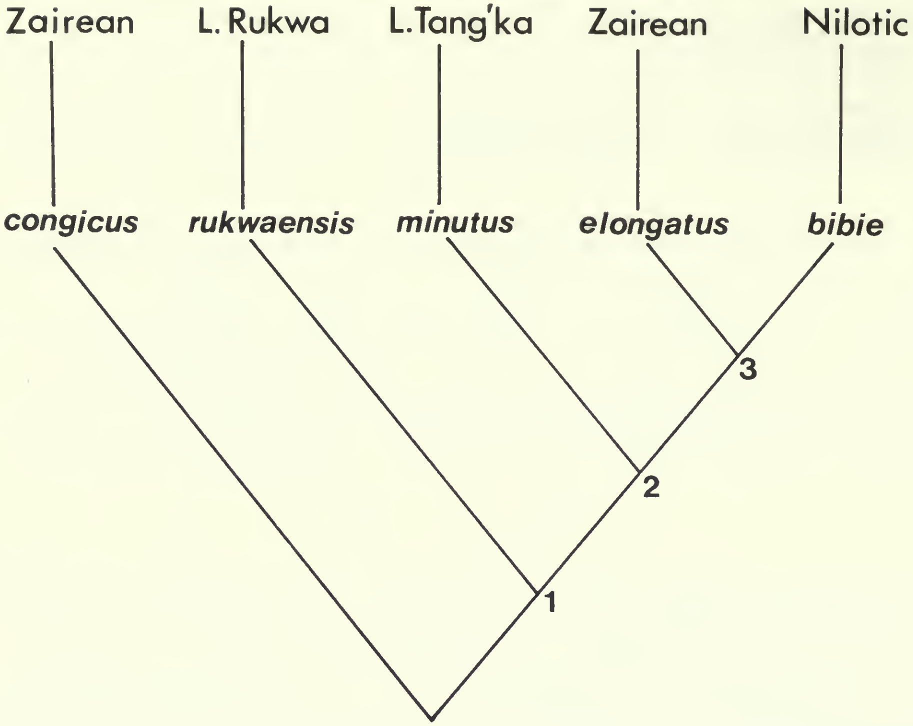

Fig. 24 Cladogram of *Chelaethiops* species. Synapomorphies are 1, A_1*post* inserts entirely into the dorsal aponeurosis of A_1*ant*, well-developed frontal canal openings; 2, ethmoid region elongated, dentary with convex margin, articular face of 1st centrum prominently rounded, maxillary valve of increased width; 3, highly developed aponeurotic connection between A_1*ant* and A_1*post*, elongate axial scales.

The plesiomorphic cyprinid condition of the *adductor mandibulae* A_1 is an undivided element with a simple insertion on the maxilla (see Takahasi, 1925; Howes, 1982 : 311). The only other cyprinids known to possess a divided A_1 are certain bariliines (see below).

Another, assumed, synapomorphy is the loss of the single pair of uroneurals in the caudal skeleton. All neoboline genera lack these elements that are present in all other cyprinid taxa examined or documented; the only known exception is *Engraulicypris sardella.* It would appear that several sets of uroneurals is a primitive teleost character (see Patterson, 1968). Amongst other otophysans, characoids have up to 3 pairs, and in siluriformes, they are consolidated with other elements of the caudal skeleton (see Fink & Fink, 1981). In those cyprinid genera considered to be plesiomorphic (*Opsariichthys, Opsaridium, Barilius*), the paired uroneurals are elongate bones extending to the base of the 5th hypural. In the majority of cyprinid taxa the bones are short, triangular or curved elements. On grounds of commonality amongst cyprinids, the loss of paired uroneurals in neobolines should probably be looked upon as a synapomorphy.

Relationships of neoboline genera

A series of further derived states of those synapomorphies listed above together with other derived features relate the neoboline genera in the following pattern:

Neobola and *Chelaethiops* share:

1. *A derived form of the lateral ethmoid.* The dorsal part of the outer wall of the lateral ethmoid is produced anteriorly as a 'shield' covering the posterior portion of the olfactory

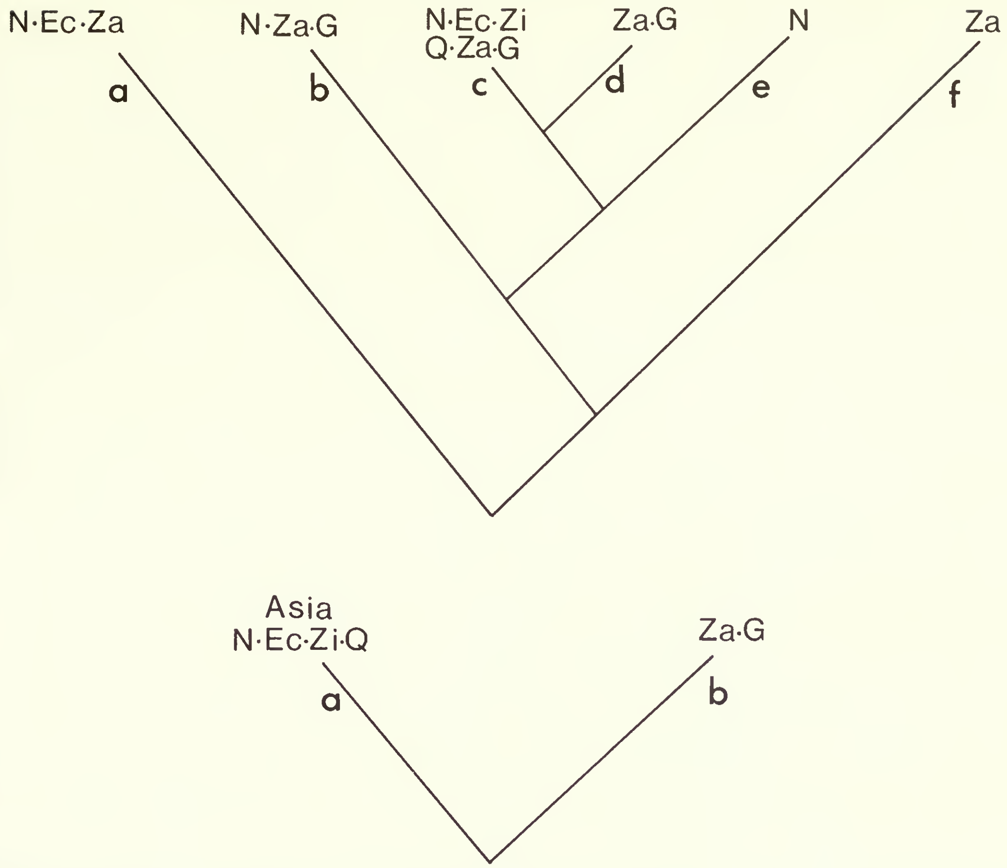

Fig. 25 Reduced area cladograms of (above) Vari's (1979) scheme of distichodontid and citharinid relationships; a–f indicate a = Citharinidae, b = Distichodontidae, Vari's (fig. 47) genera D–E; c = genera G–I; d = genera J–Q; e = *Paradistichodus;* f = *Xenocharax*; (below) Parenti's (1981) scheme for Old-World aplocheiloids, a = other aplocheiloids; b = *Aphyosemion.* Area abbreviations are as in Fig. 23.

organ (see p. 152 & Fig. 4). Elsewhere amongst cyprinids this condition is known only in *Salmostoma,* but here it is the entire lateral ethmoid wall, rather than just the dorsal part, that extends forward. This is probably a parallelism with neobolines in view of the opposing synapomorphy scheme of *Salmostoma* among chelines (see Howes, 1979; 1983).

2. *An aponeurotic constriction of muscle segment A_1ant.* This configuration of the muscle may be a mechanical device allowing A_1 to circumvent the eye. Otten (1981) presents a diagram hypothesising the functional advantage of A_1 having an aponeurotic sheet in just such a position as occurs in *Neobola* and *Chelaethiops.* In *Chelaethiops* there is a further derived state whereby the aponeurosis is bifurcated.

3. *Enlarged frontal pores opening laterally.* Those in *Chelaethiops* are all laterally directed and the frontal canal is raised above the level of the supraorbital so forming a pronounced ridge in some species (Fig. 19).

4. *Hypertrophied supraneurals.* The supraneurals are plate-like elements. In *Chelaethiops* the bones are larger than in *Neobola*, their most extreme form is encountered in *Chelaethiops minutus* where the anterior 3 or 4 are articulated in a similar fashion to those in some chelines (see Howes, 1979). The presence in *Chelaethiops* of a condylar face on the 1st centrum suggests the facility of cranial elevation, again as in chelines.

Mesobola and *Rastrineobola* share:

1. *A derived ethmovomerine morphology. Mesobola* and *Rastrineobola* both have a deep mesethmoid indentation which in *Mesobola* is V-shaped and in *Rastrineobola* omega-shaped (see p. 173). In both genera the arms of the mesethmoid abut on long, anteriorly directed preethmoids which, in effect, extend the depth of the indentation. The mesethmoid indentation is floored by the vomer which in both genera is often perforated, the foramen may be small or may coincide with the rim of the overlying mesethmoid. There are also dorsal protruberances of the vomer on either side of the medial notch (Figs 3D & E).

2. *An elongate symplectic.* The cyprinid symplectic is usually a near-triangular bone (the base of the triangle abutting on the lower tip of the hyomandibula). This form of symplectic occurs in *Neobola* and *Chelaethiops* (Figs 9A & B), but in *Mesobola* and *Rastrineobola,* the bone is elongate and horizontal rather than forming the usual steep angle (Figs 9C & D). The tips of the symplectic are spatulate.

3. *A derived jaw morphology.* The maxilla in *Mesobola* and *Rastrineobola* has a tall mid-lateral (palatine) ascending process. In this respect the form of the maxilla is near to that postulated for the presumed plesiomorphic cyprinid type (see Howes, 1981: 28). That this is a secondarily derived form in *Mesobola* and *Rastrineobola* is suggested by the following observations: (i) In *Chelaethiops* and *Neobola,* the sister-taxa to *Mesobola* and *Rastrineobola,* the upper jaw bones are long and slender; the maxilla having a long, low palatine process. This is the characteristic morphology for all bariliines and chelines, considered as the close relatives of the neobolines (see below); (ii) There is a marked concavity of the posterior border of the palatine process, and an acute lateral curvature. These features are absent in plesiomorphic cyprinid maxillae, but present in bariliine and cheline taxa; (iii) The presence of a transitional sequence in *Mesobola* species. In *M. spinifer* the palatine process is long and low, but even so is still higher than that of *Neobola, Chelaethiops* and bariliines. In *Mesobola brevianalis* and *M. moeruensis,* the process is taller and more triangular, and in *Rastrineobola,* the palatine process is best developed (Figs 9D–G).

In *Mesobola* and *Rastrineobola* the dentary is deep with a convex dorsal border, a feature particularly marked in *Rastrineobola* (Fig. 8E). In both genera the anguloarticular is long with a horizontal dorsal surface. The usual cyprinid condition, exemplified by *Neobola* and *Chelaethiops* (Figs 8A & C), is for the anguloarticular to be short and deep with a sloped or concave dorsal border. This condition also appears general for teleosts (see Nelson, 1972). In *Rastrineobola* the jaw articulation is situated so far forward that it lies below the anterior half of the orbit (*cf.* below, or posterior to the centre in other neobolines). Only in *Engraulicypris,* amongst bariliines, is the jaw articulation so far forward (see below).

A feature also shared by *Mesobola* and *Rastrineobola* is the elongation and ventral curvature of the posterior chamber of the swimbladder. Comparative out-group data is too sparse to recognize this feature as a synapomorphy, but a brief survey of cyprinids suggest the condition is, at least, unusual.

In summary *Neobola* and *Chelaethiops*, and *Mesobola* and *Rastrineobola* form paired sister groups related on a synapomorphy scheme involving ethmovomerine, frontal, jaw bone, suspensorial and jaw muscle morphology (Fig. 20). The relationships of the neobolines are with certain bariliines.

Relationships of the neoboline group

The neobolines share with the bariliine genera *Engraulicypris, Leptocypris, Raiamas* and *Opsaridium* the following synapomorphies:

1. A divided *adductor mandibulae* A_1 muscle. In *Leptocypris* and *Engraulicypris* the fibres of A_1*post* insert partly into the fascia of A_{11}*ant* and partly into the rictal tissue as in the neobolines. In *Raiamas, Opsaridium* and South-East Asian *Barilius,* all the fibres of A_1*post* insert into the fascia of A_1*ant* (Fig. 15), a condition taken to represent the predecessor of the more complex arrangement in the neobolines, *Leptocypris* and *Engraulicypris.*

2. *Pectoral and pelvic axial scales.* Howes (1983) proposes a fundamental dichotomy of the bariliine group based on axial scale type (*viz*: elongate 'typical' scales *versus* modified scales in the form of fleshy lobes). Amongst the neobolines, axillary scales are reduced in some species of *Mesobola* and are lacking in *Rastrineobola.* In bariliines, axillary scales are absent in *Engraulicypris.* From the widespread distribution of axial scales amongst neoboline and bariliine genera, it is assumed that their absence in those above cited taxa are independent losses. Where scales are reduced or absent, this condition is confined to lacustrine species.

3. *Derived ethmovomerine morphology.* Amongst the bariliines, only *Leptocypris* and *Engraulicypris* have an ethmovomerine architecture approaching that of the bariliines. In neither genus is there a dorsal channelling of the supraethmoid as in neoboline genera, but in *Leptocypris* there is a slight lateral elevation of the bone (Fig. 3F). In some *Leptocypris* species and in *Engraulicypris* there is an omega-shaped ethmoid indentation, anterior elongation and perforation of the vomer (see Howes, 1980; 1983). These are features shared with the neobolines *Mesobola* and *Rastrineobola.* This pattern of ethmovomerine morphology is disjunct throughout *Leptocypris, Engraulicypris* and neoboline species and may, therefore, be a case of homoplasy. Likewise, a somewhat channelled supraethmoid occurs in a group of South-East Asian and Indian *Barilius* species. In these taxa, however, the ethmoid bloc is depressed, rather than laterally compressed as in the neobolines, and other characters such as tubercle pattern and palatine morphology suggest that they form a lineage distinct from that of the neobolines, *Leptocypris* and *Engraulicypris.*

One other feature to be considered is the absence in *Engraulicypris* of paired uroneurals. It was noted above (p. 178) that these elements are lacking in all neoboline genera, and their loss might be construed as a synapomorphy. If this is the case, then *Engraulicypris* would appear to be the sister group to the neobolines, thence to *Leptocypris.* In the synapomorphy scheme presented here (Fig. 20), the caudal fin character has been reserved until such time as more complete comparative data on its distribution are available.

In summary, the neobolines form the sister group to that comprising *Leptocypris* and *Engraulicypris*, which in turn is the sister group to *Raiamas.* This combined assemblage comprises the sister group to the South-East Asian bariliines (possibly including some Indian *'Barilius'* and *Opsaridium.*

Neoboline distribution and its biogeographic implications

Neoboline taxa have a wide distribution in Africa, embracing the 'ichthyofaunal provinces' Roberts (1975) termed Nilo-Sudanian, East Coast, Guinean, Zambesian and Zairean. *Neobola* species occur in eastern flowing rivers of Ethiopia and Somalia, northern Kenya and in Lake Turkana (Fig. 21). *Chelaethiops,* the derived sister group of *Neobola*, is extensively distributed throughout the Zairean, Guinean and Nilo-Sudanian provinces and also includes Lakes Tanganyika and Rukwa (Fig. 21). *Mesobola* is present in Lake Albert, the Malagarasi, Rufiji and Zambesi systems, and eastern flowing rivers as far south as Natal (Fig. 22). The genus is also known from the Orange River on the western side of Africa, although there is some doubt about the record from the Cunene River; see p. 170. *Rastrineobola* occurs only in the Lake Victoria basin–including Lake Kioga (Fig. 22).

The most notable feature of neoboline distribution is the geographical division of the genera by the eastern Rift system, so that *Chelaethiops* is the only genus with a continuous westward extension. When depicted as an area cladogram, the branching sequence of neoboline taxa shows a sister-group relationship between Nilotic and Zairean areas and East-Coast and Zambesian (Fig. 23). The sister group of the neobolines, *Leptocypris+ Engraulicypris,* display a congruent area pattern, with Lake Malawi forming the sister-area to the Nilo-Zairean (Fig. 22). Within *Leptocypris,* those species considered as derived, *weynsii, lujae* and *modestus,* are Zairean, again a pattern in agreement with that of the derived neoboline, i.e. *Chelaethiops,* species; see below.

On the eastern side of the Rift, the area relationship signified by the sister group *Mesobola* + *Rastrineobola,* is between East Coast-Zambesian + Lake Victoria basin.

The distributional pattern of these sister-group pairs is readily explicable on vicariance events involving, in the case of *Neobola* and *Chelaethiops*, the formation of the Rift system, and, in that of *Mesobola* and *Rastrineobola,* the isolation of the latter in the Victoria basin. Roberts (1975) includes Lake Victoria in the East-Coast province, and this geographical relationship is certainly borne out by the neoboline phylogeny.

Chelaethiops also occurs in both the Malagarasi and Lake Rukwa. This distribution can either be interpreted as a subsequent dispersal from Lake Tanganyika or, as representing the result of an interrupted (vicariant) distribution due to the topographical evolution of that lake; see Banister & Clarke, 1980. The synapomorphy scheme of *Chelaethiops* species (Fig. 24) makes the latter interpretation more economical. *Chelaethiops congicus* (Zairean) has least derived features and together with *C. rukwaensis* (Lake Rukwa and Malagarasi) and *C. minutus* (Lake Tanganyika) forms the sister group to the derived species *C. bibie* (Nilo-Sudanian) and *C. elongatus* (Zaire-Guinean); see Fig. 24 for character summary.

Mesobola occurs sympatrically with *Chelaethiops* in the Malagarasi drainage and the Lualaba, it is also disjunct in distribution, being found in the Orange River below the Aughrabies Falls on the western side of the continent. There is a single, unconfirmed record of its presence in the Cunene (see p. 170). Roberts (1975 : 309) supposed this distribution to be the result of dispersal through South-West Africa. It would be more parsimonious to recognise in this pattern the fragmentation of a formerly uninterrupted distribution.

In terms of historical biogeography, the neobolines seem uninformative. This is due partly to the genera resolving only into two-area cladograms, and the mostly unresolved interrelationships of their contained species. Indeed, for *Mesobola,* a species cladogram cannot be constructed as the species are presently recognised only on the basis of mainly, meristic differences. For *Neobola,* of the three species, one, *N. fluviatilis,* is possibly a population variant of another, *N. bottegi*, and the third, N. *stellae* is a lacustrine endemic. The other reason is that there are few cladograms of African freshwater fishes which can be used in broader comparison with neobolines. Only three phylogenies can be considered as a basis for constructing area cladograms; those of Vari (1979), Parenti (1981) and Howes (1983).

Vari (1979) studied the characoid families Citharinidae and Distichodontidae, recognising them as sister groups. Both families are widespread throughout Nilo-Sudanian, Guinean, Zairean, East-Coast and Zambesian provinces. Within the Distichodontidae, most taxa, which according to Vari's scheme of interrelationships are the derived ones, occur in Zairean and lower Guinean regions. As a simplified area cladogram, the distichodontid pattern is one of repeated dichotomy between Nilotic and Zairean-Guinean regions (Fig. 25).

Parenti's (1981) geographical analysis of African aplocheiloid cyprinodonts demonstrates a sister-group relationship between Zairean-Guinean (derived forms) and Nilo-Sudanian, Zambesian-East Coast and Quanzan provinces (Fig. 25).

The bariliine relationships presented by Howes (1980; 1983) show both *Opsaridium* and *Raiamas* with Asiatic relatives and representatives. *Opsaridium* has as its sister group the South-east Asian *Barilius* (and possibly some Indian species, see above, p. 180), and *Raiamas* is represented also in India and Burma. At this high level of universality, the pattern of bariliine distribution is virtually concordant with that presented by Parenti (1981) for Old World aplocheiloids (*cf.* fig. 23 in Parenti with fig. 47 in Howes, 1980). Interestingly, all these patterns – aplocheiloids, characoids, bariliines and neobolines – exclude the Cape Province (see below).

African ichthyogeography and biotic subdivision

Too few data are available to form any refined picture of African ichthyogeographical history. Those that are available suggest a widespread, plesiomorphic fauna disrupted by a Zairean-Nilotic break with a subsequent (or even contemporaneous) Zairean-Guinean fragmentation.

To date, studies of African ichthyogeography have been little more than catalogues of endemism and scenarios of dispersals (see Greenwood, 1983 for discussion). The various hypotheses proposed for African freshwater fish distribution are *ad hoc* assumptions based on the supposedly known histories of past drainage patterns. An example of this approach is given by Livingstone *et al* (1982) who account for fish distribution patterns by invoking dispersal from refugia, competition and 'powers of dispersal'. These authors find the '. . . pattern of faunal similarities surprising . . . ' and rather than accepting that this pattern reflects a previously uniformly distributed fauna (Greenwood, 1983) would prefer to see in it a reflection of '. . . more recent faunal exchange'.

The same problems have beset discussions of the biogeography of other African faunas and, as for fishes, ecological parameters are seen as the determinate factors in shaping distributional pattern. Two recent examples are works dealing with molluscs (Brown, 1978) and birds (Crowe & Crowe, 1982). According to Brown '. . . many distributional patterns seem to be dependent mainly on existing ecological conditions'. He does, however, draw attention to the taxonomic relationships between southern east African and Malagasian molluscs. Crowe & Crowe correlate their avian zones with vegetation types, although admitting that the distributional patterns of passerine and non-passerine birds cannot be explained solely on environmental factors; there is no reference to the possible phylogenetic relationships of the respective bird groups.

Similarly, the reasoning behind accounts for mammal distribution has been entirely ecological. Indeed, Rautenbach (1978) emphasises that faunal interrelationships should be interpreted from an ecological point of view. No consideration has been given to a vicariographic approach.

There is a cladistic analysis of African bufonids by Grandison (1981) which shows that the plesiomorphic lineage, represented by *Capensibufo*, is restricted to Cape Province. A reduced area cladogram of the other bufonid taxa also reveals repeated east-west dichotomies. Interestingly, Grandison remarks of *Capensibufo* that it may '. . . have had an austral origin'.

It was noted above that some groups of cyprinids, characoids and cyprinodonts are congruent in their distribution in being absentees from the Cape Province. The relationships of those freshwater fishes endemic to the Cape are at present largely unknown. According to McDowall (1973) the South African galaxiid, *Galaxias zebratus,* may have a close phylogenetic relationship with *Brachygalaxias bullocki* in Chile, although McDowall would prefer to recognize any affinity between the two as convergence. Reid (pers. comm.) has pointed out that the *Labeo umbratus* group of the Cape may be more closely related to Asian than to other African *Labeo* species.

The ichthyofaunal peculiarities of the Cape are paralleled by its flora. Miller (1982) in reviewing bryophyte distribution concludes that the Cape was '. . . an island which was left behind and later caught up with the primary continental block . . . '

It is clear that if the phylogenetic relationships of the endemic Cape fishes were resolved, a general biogeographic pattern for this region would begin to emerge. This example serves to underline Greenwood's (1983) thesis that only by resolving the phylogenetic relationships of African freshwater fishes will any understanding be gained of their present-day distributional patterns.

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British Museum (Natural History)

Tilapiine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

The tilapias are cichlid fishes of Africa and the Levant that have become the subjects of fish-farming throughout the warm countries of the world. This book described 41 recognized species in which one or both parents carry the eggs and embryos in the mouth for safety. Substrate-spawning species, of the now restricted genus *Tilapia*, are not treated here.

Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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The haplochromine species (Teleostei, Cichlidae) of the Cunene and certain other Angolan rivers

Peter Humphry Greenwood

Zoology series Vol 47 No 4 27 September 1984

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The haplochromine species (Teleostei, Cichlidae) of the Cunene and certain other Angolan rivers

Peter Humphry Greenwood
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Introduction

> *L'Angola est un plateau d' où descendant de nombreux*
> *fleuves et rivières qui cachet encore bien des secrets* Poll (1967:16)

Despite Poll's (1967) extensive monograph on the fishes of Angola, and the work of Trewavas (1964, 1973) and Bell-Cross (1975) much has still to be learnt about the biology, taxonomy and zoogeography of the haplochromine cichlid species in this region of Africa (see Greenwood, 1979). A basic inventory of the species has been worked out, but many taxa are known only from the type specimen, by a limited number of type specimens or by some specimens whose locality is recorded no more precisely than 'Angola'. Above all, almost nothing is known about the phyletic relationships of the species, and hence zoogeographical conclusions based on them are correspondingly uncertain.

Judging from the present-day hydrography of Angola, especially the isolated rivers which discharge directly into the Atlantic, and the numerous tributaries emptying into the Zaire system, one might expect a high degree of localized endemicity in the various rivers. In other

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words, the physical background would seem ideal for promoting vicariant speciation, a situation that is, indeed, suggested by some of the taxonomic data already available.

Thus it was with considerable pleasure and interest that I accepted an invitation from Dr M. Penrith (then of the Windhoek Museum) to study a large collection of cichlid fishes from, principally, the Cunene river. The Cunene is one of the least studied Angolan rivers, and physiographically is one of the most isolated in the country. The collection has provided an opportunity to redescribe a number of species on the basis of many more specimens than were previously available, and to confirm the presence in the Cunene of species either not previously recorded from there or recorded with some uncertainty. Also, it has established that several species have an extensive distribution within the river itself, their ranges stretching from or near the river mouth, almost to its northernmost tributaries.

Less has been learnt about the relationships of the endemic Cunene species, and the collection has underlined the still unsatisfactory taxonomic situation surrounding species of the *Serranochromis* subgenus *Sargochromis*. However, a species currently of indeterminable status '*Haplochromis*' *welwitschii* (Blgr), whose type specimen is probably from the Cunene, can now be referred to the genus *Chetia*, a taxon otherwise known from the Limpopo system in South Africa (see Appendix II), and a tributary of the Zaire system (see Balon & Stewart, 1983). In terms of species numbers and morphological diversity, the Cunene seems to have a haplochromine fauna more complex than that in any other Angolan river and, indeed, more diverse than that of the Zambezi-Kafue systems. The new collection also apparently corroborates existing ideas that the Cunene fauna, on a broad zoogeographical scale, has phyletic affinities with both the Zaire and the Zambezi drainage systems (Trewavas, 1964, 1973; Bell-Cross, 1975; Roberts, 1975). However, sister-group relationships for the endemic haplochromines both within and outside the different sytems still cannot be established. Zoogeographical problems are compounded by the fact that precise specific identification is impossible for most Cunene representatives of the *Serranochromis* (*Sargochromis*) species complex, and is unlikely to be obtained until more specimens, coupled with data on male breeding colours, are available from the different river systems within and outside Angola.

Methods and materials

Methods. Measurements and counts generally are those used in my other papers on haplochromine fishes (see Greenwood, 1981). Measurements relating to the neurocranium are those used in Greenwood (1980: 4–6); an additional measurement used here, ethmovomerine length, is taken directly from the anterior tip of the vomer to the most ventrolateral point on the lateral ethmoid bone.

When the length of the ascending premaxillary process is given for whole specimens it is measured directly from the dentigerous surface of the bone, between the teeth on either side of the midline, to the distal tip of the processes (determined through the skin by moving the premaxillae gently forwards and downwards). When this length is taken from a skeletal preparation, the depth of the dentigerous arm is excluded, and the reference points are those illustrated in Greenwood (1980: 5, fig. 2), *viz* from the distal tip of the processes to a horizontal line drawn level with the upper margin of the dentigerous arm immediately posterior to the basal region of the ascending processes.

Measurements of the lower pharyngeal bone are those employed by Bell-Cross (1975: 410), *viz*: length is taken along the median axis of the bone, from the anterior tip of its shaft to a line drawn transversely between the tips of the posterior horns. Lower pharyngeal breadth is measured directly between the outer edges of the two horns.

A feature not previously mentioned in the description of haplochromine species is the *anal sheath scales*. My attention was drawn to these scales when examining part of the type series of *Tilapia steindachneri* Blgr (see p. 190). In these specimens, a distinct but shallow sheath of small, almond-shaped scales, aligned in a single row, lies between the anal fin base and the ventral row of body scales. The long axes of the scales are arranged horizontally, and the scales are either imbricate or spaced, sometimes widely spaced.

It seems that anal sheath scales occur in a number of haplochromine lineages. A sheath, or at least some characteristically almond-shaped scales, has been found in species from Lakes Victoria, Tanganyika and Malawi, as well as in some fluviatile taxa. Sheath length varies intraspecifically to a considerable extent. It can be present along almost the entire base of the fin, or it may be confined to the base of the spinous part (apparently the commonest condition). Often it is represented merely by a few isolated scales. Since the scales are easily dislodged, the latter condition may be artefactual.

The taxonomic value of the anal sheath, in whatever form it is present, cannot yet be assessed.

Materials. All the type specimens of Angolan haplochromine species in the BM(NH) collections were examined, as were other specimens identified as conspecific with these types or with type specimens of Angolan species held in other institutions. Likewise, all the BM(NH) material of *Serranochromis* and *Pseudocrenilabrus* species was studied, together with the type and other specimens of '*Haplochromis*' *darlingi*, a species first recorded from Angola by Poll (1967).

In addition, the following material was borrowed from the Zoological Museum of Hamburg (ZMH) and the Musée Royal de l'Afrique Centrale, Tervuren (MRAC).

ZMH 4599 *Haplochromis* species (7 specimens) Cunene R.
    4599a *Haplochromis* species (1 specimen), Cunene R. at Capelongo.
    1300 *Serranochromis angusticeps* (1 specimen), Cunene R. at Capelongo.
    1307 *Serranochromis angusticeps* (1 specimen), Cunene R. at Capelongo.
    1718 *Serranochromis robustus jallae* Cunene R. at Mülongo Fürt.
    1719 *Serranochromis thumbergi* (2 specimens) Cunene R. at Capelongo.
The identity of all these *Serranochromis* specimens has been confirmed.
    1722 *Haplochromis frederici* (4 specimens), Cunene R. at Capelongo. Two specimens are members of the *Serranochromis* (*Sargochromis*) *giardi-codringtoni* complex (see pp. 217–224 below), and two probably can be referred to *S.* (*Sargo.*) *coulteri* (Bell-Cross).
Musee Royal de l'Afrique Centrale (MRAC), Tervuren.
MRAC 154779–780 *Haplochromis welwitschii*, Sanguenque Uembe Cûanaa, Angola.
MRAC 66470 *Haplochromis schwetzi,* holotype, Cuango R., Angola.
MRAC 163992; 164013–016; 164023–026; 164027–032; 164033–39 *Haplochromis schwetzi*, paratypes (26 specimens), Cuango R., Angola.
MRAC 163981–986 *Haplochromis darlingi*, Lac Calundo, Angola.

Other material examined is listed in the text. Regrettably, as a result of extensive reorganization now been carried out in the fish collections of the Vienna Museum, it was impossible to examine the types of two Steindachner (1866) species: *Chromis humilis* and *Chromis acuticeps.* Both taxa are described, simply, as coming from Angola. Fortunately the types of both species were carefully examined by my colleagues Dr Ethelwynn Trewavas, and later by Mr G. Bell-Cross (now of the Port Elizabeth Museum, South Africa). I have been able to use the notes and recollections of both these people, to whom I am most indebted.

The haplochromine species of the Cunene river

THORACOCHROMIS Greenwood, 1979

Several Angolan species, currently referred to the genus *Haplochromis,* show the diagnostic features of *Thoracochromis*, *viz* an abrupt size change between the small scales on the chest and the larger scales on the ventrolateral aspects of the flanks, a marked anteroventral embayment of the cheek squamation (with, in some species, a narrow, horizontal naked area lying between the cheek scales and the preoperculum), and the absence of true ocelli, but not discrete spots, on the anal fin or adult males (see Greenwood, 1979: 290–292).

The Angolan species now placed in *Thoracochromis* are: *Haplochromis lucullae* (Blgr), 1913; *H. albolabris* Trewavas & Thys van den Audenaerde, 1969; *H. schwetzi* Poll, 1967, and *H. buysi* M.-L. Penrith, 1970.

Haplochromis lucullae was treated as a junior synonym of *H. acuticeps* (Steindachner, 1866) by Regan (1922: 255), but the species has been informally 'resurrected' by several recent authors, notably Trewavas (1964: 8–9, 1973: 31), Penrith (1970: 170–171) and Bell-Cross (1975: 427). Unfortunately, I have not been able to examine the holotype of *H. acuticeps* (see p. 189) but from Dr Trewavas' comments, based on detailed examination of that specimen, its separation from *lucullae,* at least at the species level, is justified (see also Trewavas, 1973: 31). Regrettably, neither Steindachner's (1866) original description, nor Trewavas' later reexamination of the *acuticeps* type specimen provide any information on the nature of the size-change at the chest-abdominal scale transition line, nor are there data on the nature of the cheek squamation. Thus it is impossible to comment on the generic assignment of '*acuticeps*'. Steindachner's figure, however, suggests that the scale transition is of the *Thoracochromis* type.

With one exception (*Th. schwetzi*), and unlike species of *Thoracochromis* from the Nile, Lake Turkana and the Zaire river system, none of the Angolan species has more than 4 or 5 upper lateral line scales each separated from the dorsal fin base by one large and one small scale. This low number is thought to represent the primitive condition, the higher number (8 or 9 scales) occurring in the other species being the derived one (Greenwood, 1979: 291). As compared with the Nilo-Zairean taxa most Angolan species have more scales in the lateral-line series and higher modal counts for this feature. Again, an exception is *Th. schwetzi*, whose lateral line counts are like those in the Nilo-Zairean species; interestingly, *Th. schwetzi* occurs only in the Cuango river, an Angolan affluent of the Zaire system.

In all other meristic and morphometric features the Angolan *Thoracochromis* do not lie outside the range of variability found in other members of the genus. The significance, if any, of the differences in squamation cannot be assessed until more data are available from those Angolan species which are currently represented only by one or a few type specimens.

Species previously referred to *Haplochromis* and which are not members of *Thoracochromis*, are discussed in Appendix I.

Thoracochromis buysi (Penrith), 1970

SYNONYMY *Haplochromis buysi* Penrith, M.-L., 1970. *Cimbebasia,* ser A, **1** (7): 168–171, plate 2; fig. 1. Holotype: SM5099, a specimen 75 mm standard length, from the Cunene river mouth. Paratype: SAM 25243, a specimen 61 mm SL from the same locality. This specimen is now damaged extensively, and was not used in the redescription of the species. It is, however, conspecific with the holotype.

Tilapia steindachneri (part) Boulenger, 1913. *Ann. Mag. nat. Hist.* (8) **12:** 483. Five of the syntypical specimens only (BMNH 1907.6.29:141–5, from the Que river). The largest specimen, 104.5 mm SL, alone is in reasonable condition. Although Boulenger (1913) did not select a holotype, he did later (1915) designate one specimen as 'Type' in the caption to a figure of that specimen. The fish in question is one of the syntypes from Mossamedes which Regan (1922) included in the species *Sargochromis mellandi.* Thus the inclusion of the five Que fishes in the synonymy of *Thoracochromis buysi* (Penrith), 1970 raises no question of nomenclatural priority for Boulenger's earlier name '*steindachneri*'.

Haplochromis acuticeps (part): Regan, 1922. *Ann. Mag. nat. Hist.* (9) **10:** 255 (the syntypical specimens of *T. steindachneri* noted above; BMNH 1907.6.29:141–5).

DESCRIPTION. Based on 46 specimens, including the holotype, 44·0–118·0 mm standard length.

Depth of body 29·4–34·7 (M = 32·0)% of standard length, length of head 30·4–36·4 (M = 31·5)%.

Dorsal head profile gently curved (almost straight in a few specimens), sloping at an angle of 35°–40° to the horizontal, the angle increasing with the fish's size. The upper margin of

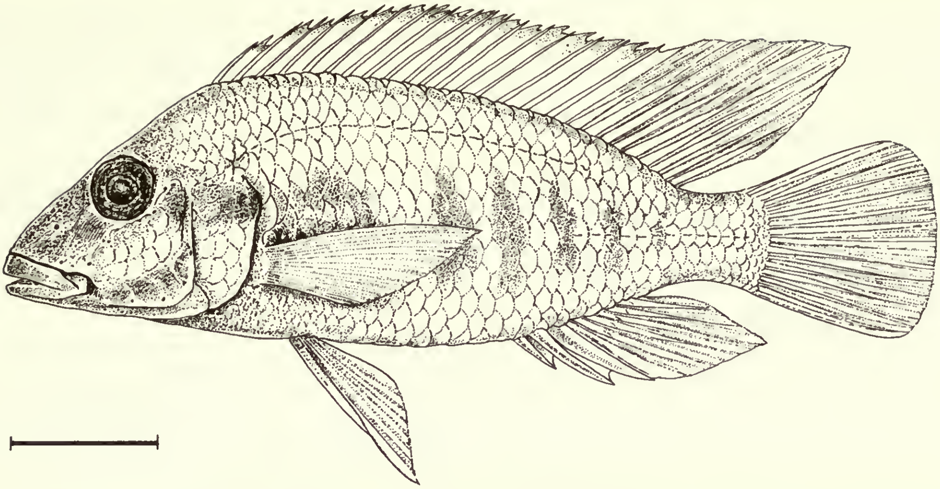

Fig. 1 *Thoracochromis buysi.* Adult male (1984.2.6: 24). Drawn by G. J. Howes. Scale = 20 mm.

the eye is coincident with, or lies immediately below the dorsal profile of the head, but never extends above it. The extent to which the curve of the profile is interrupted by the intrusion of the premaxillary ascending process varies, but is never marked and may be influenced by preservation methods.

Preorbital depth 18·5–26·0 (M = 22·9)% of head length, showing slight positive allometry with standard length; least interorbital width 16·6–23·6 (M = 19·4)% of head. Preorbital depth is generally greater than least interorbital width, but in some individuals the measurements are equal; in no specimen examined is the interorbital width greater than the preorbital depth (cf. *Th. schwetzi* where the interorbital is wider than the preorbital is deep).

Snout length shows clear cut allometry with standard length. The range for the whole sample is 31·0–39·0% of head; in specimens less than 70 mm SL (n = 17) it is 31·0–35·3 (M = 33·1)% and in larger individuals (71·0–118·0 mm SL, n = 29) it is 34·5–39·0 (M = 36·7%). The snout is from 1·0–1·3 times longer than broad (modal range 1·0–1·1).

Eye diameter is negatively allometric with standard length; for the whole sample it is 25·4–36·2% of head length, in fishes < 70 mm SL it is 28·6–36·2 (M = 33·6)%, and in larger individuals 25·4–33·3 (M = 28·3)%.

Cheek depth is 18·2–27·8 (M = 22·7)% head, and shows no obvious allometry with standard length.

Caudal peduncle length is 16·2–22·0 (M = 19·0)% of standard length, and 1·3–1·9 (modal range 1·5–1·7) times its depth.

Mouth horizontal or almost so, the lips slightly but noticeably thickened, the jaws equal anteriorly. The posterior tip of the maxilla reaches a vertical closer to the anterior orbital margin than to the nostril, rarely extending to a vertical through the margin of the orbit.

Lower jaw 1·5–2·0 (mode 1·8) times longer than broad, its length 33·3–39·0 (M = 36·0)% of head length. Ascending processes of the premaxilla 25·7–34·3 (M = 30·6)% of head.

Gill-rakers and pharynx. There are 8–10 (mode 10), relatively short and moderately stout gill-rakers in the outer row on the lower part of the first arch; the lowermost one or two rakers are smaller than the others. The rakers are transversely elongate, with the upper surface produced into two or three cusp-like projections. Microbranchiospines are present.

In his original description of *Tilapia steindachneri* (see synonymy above), Boulenger (1913) gave the gill-raker count as 13–14, a count repeated in his redescription of 1915. These figures, however, apply only to those syntypes which Regan (1922) ultimately referred to *Sargochromis mellandi.* The remaining syntypes, which I refer to *Th. buysi*, have only 9 or 10 rakers.

The dorsal pharyngeal epithelium is thickened and thrown into well-defined, approximately longitudinal furrows, the crests of the ridges often further developed into low papillae. Immediately anterior to the toothed upper pharyngeal bones of each side, the buccal roof is produced into a prominent pad which, however, has neither the size nor the shape of the visor-like hanging pad found in certain cichlid genera (see Trewavas, 1974: 389–392, and Greenwood, 1983: 265–267).

Scales are ctenoid below the level of the lower lateral-line, cycloid above it and on the chest. The chest scales are small, except for a midventral row of slightly larger scales, and are noticeably smaller than those on the ventrolateral aspects of the flanks and on the belly. The size transition is abrupt and takes place along a line connecting the pectoral and pelvic fin insertions, or a little behind that line.

There are 32 (rare) to 36 (rare) scales, modally 34, in the lateral-line series, $4\frac{1}{2}$–$6\frac{1}{2}$ (modally 5 or $5\frac{1}{2}$) between the dorsal fin origin and the upper lateral-line, and 7–9 (mode 8) between the pectoral and pelvic fin bases. Cheek with 3–5 (mode 4) scale rows, the scaled area with a clearly demarcated, naked embayment anteroventrally. Each of the last 3 or 4 pored scales in the upper lateral-line is separated from the dorsal fin base by one large and one small scale.

Fins. Dorsal with 14 (f1), 15 (f17), 16 (f26) or 17 (f2) spinous and 10 (f2), 11 (f24), 12 (f18) or 13 (f2) branched rays. Anal with 3 spinous and 7 (f8), 8 (f37) or 9 (f1) branched rays.

In all but three of the 46 specimens examined, small, almond-shaped sheath scales are present at the base of the anal fin (see p. 188 above). The horizontal extent of these varies from a row extending along the entire spinous part of the fin and reaching the 3rd–5th branched ray, to a few isolated and often non-imbricating scales at the base of either or both the spinous and the anterior part of the soft fin; sometimes only one or two scales are present and then usually at the base of the first one or two spines.

The pectoral fin length is 19·6–26·4 (M = 21·1)% of standard length, 61·3–80·0 (M = 70·2)% of head length. The pelvic fins have the first branched ray longer than the second, most noticeably so in adult males, but never produced into a filamentous extension, and never reaching to the origin of the anal fin.

The caudal fin generally is subtruncate, but is almost truncate in a few specimens; it is scaled on its proximal third to half.

Teeth. The *outer row* in both jaws of fishes up to *ca* 90 mm SL is composed, mostly, of relatively slender, unequally bicuspid and gently recurved teeth. The small minor cusp is angled away from the vertical axis of the major cusp (Fig. 2A). In teeth from the upper jaw, the tip of the major cusp usually lies within, or but slightly beyond, the vertical formed by the outer margin of the tooth; in lower jaw teeth, however, the tip often lies well outside that line, as it may occasionally do in upper jaw teeth as well.

Posteriorly in the premaxillary outer row of most specimens there are from 2 to 8 unicuspid teeth. These teeth, unlike those in *Astatotilapia* (see Greenwood, 1979), are not noticeably enlarged nor are they caniniform.

Although some unicuspids are present laterally and anteriorly in the jaws of fishes less than 90 mm SL (especially those in the 75–90 mm range), their frequency only increases in specimens over 90 mm SL, becoming the predominant form in fishes more than 110 mm SL; even in these specimens, however, a few weakly bicuspid teeth are present in both jaws. The unicuspids are slender and slightly recurved, and do not have the near-cylindrical neck and crown of typical caniniform teeth. Both uni- and bicuspid teeth often show pronounced wear at the tip of the crown.

There are 42–66 (modal range 50–62) teeth in the outer premaxillary series, the number not showing any clear-cut allometry with the fish's standard length.

Inner series. It is difficult to generalize about tooth form in these rows because there is both a change with growth and, apparently, some inter-population differences as well.

Most fishes less than 85 mm SL have a predominance of slender tricuspid teeth in the inner rows; the median cusp of these teeth is longer and broader-based than are the cusps flanking

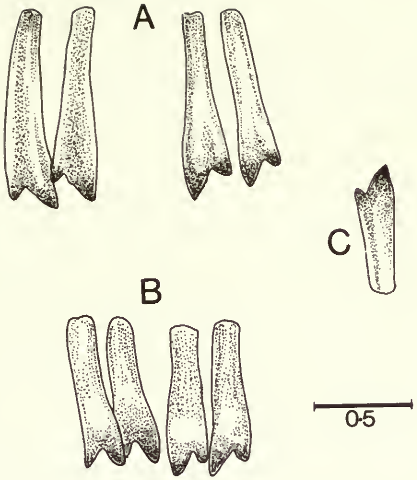

Fig. 2 Outer row jaw teeth of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. A & B are anterior premaxillary teeth, C, a tooth from the anterior part of the dentary.

it. A few slender bicuspid and weakly bicuspid, nearly unicuspid teeth are interspersed amongst the tricuspids, especially in fishes over 70 mm SL. Such teeth become more frequent in specimens between 75 and 85 mm SL. In specimens from certain localities, however, this admixture of tricuspids, weakly tricuspids and bicuspids is found in much smaller fishes, even among individuals as small as 47 mm SL.

Fishes above *ca* 80 mm SL from all localities show a further increase in the number of bi- and unicuspid inner teeth, coupled with a decline in the number of tricuspids. These latter also tend to be less distinctly tricuspid, the median cusp gaining in dominance over the lateral ones. Specimens more than 90 mm SL have an essentially unicuspid inner dentition, although a few bicuspid and weakly bicuspid teeth persist; only the largest fish examined, 118·0 mm SL, has the inner rows composed solely of unicuspids.

Anteriorly and anterolaterally the inner teeth are arranged in 2 (mode) or 3 rows, rarely in a single irregular row. Posteriorly in both jaws, however, only a single row of teeth is present.

All but a few of the specimens examined have the dental mucosa greatly thickened with the result that just the tips of the teeth are visible. That this situation is a preservation artefact, cannot be overruled.

Lower pharyngeal bone and dentition. The lower pharyngeal bone has an approximately triangular and equilateral dentigerous surface; the anterior shaft is short (Fig. 7A). Except for about the posterior four or five teeth in the median tooth rows, the pharyngeal teeth are slender, compressed and cuspidate, and are closely spaced. The exceptional teeth are distinctly coarser and larger than their lateral congeners, but still retain a cuspidate crown. Sometimes a few posterior teeth in the rows immediately lateral to the median row are slightly coarser than the other lateral teeth.

The pharyngeal bone itself is not enlarged, and has slender posterior horns.

Osteology. Neurocranium. Overall skull morphology in this species (Fig. 10A) departs slightly from the generalized haplochromine type (Greenwood, 1979: 274) in being more slender, with a shallower and narrower otico-occipital region, narrower interorbital and ethmoid regions, and in having a lower and less expansive supraoccipital crest. Also the dorsal skull profile, from the anterior tip of the supraoccipital bone to the tip of the vomer, slopes less steeply (*ca* 30° compared with *ca* 45° in the case of *Astatotilapia nubila* or *A. bloyeti*; *cf* Fig. 10A with fig. 6 in Greenwood, 1979).

Expressed as percentages of neurocranial length, the orbital depth is 34·8–36·3%, preorbital depth 17·4–20·8%, preotic skull length 63·6–66·6%, ethmoverine length 27·0–27·4%, depth of otic region 37·5–40·0%, width of otic region 50·0%, and greatest height of supraoccipital crest 16·5–18·2% (Data from three skulls, 22·0, 23·0 and 24·0 mm neurocranial length; for definition of measurements see Greenwood, 1980: 4–5).

The apophysis for the upper pharyngeal bones is of the *Haplochromis* type (Greenwood, 1978); in two of the three skulls examined the basioccipital contribution to the facet is large, but in the third it is greatly reduced.

Suspensorium (Fig. 3A). There is a distinct gap between the palatine and entopterygoid bones, an unusual features so far recorded only in members of the *Ophthalmotilapia* assemblage of Lake Tanganyika, and in at least some *Lethrinops* species (Lake Malawi); for a discussion of this feature see Greenwood (1983: 254–6, and 279).

The hyomandibula in *Th. buysi* (Fig. 3C) has a fairly well-developed anterior flange, but one which is less expansive than that in *Orthochromis machadoi* (see Fig. 3E).

Jaws. The *dentary* (Fig. 11A) is a slender bone, with its alveolar surface flared outwards so as to form a shelf-like overhang above the bone's lateral face. There is no mental projection in the symphysial region, which is, however, a little swollen.

The *premaxilla* (Fig. 8A) has no outstanding features. Its ascending processes are long (almost one fifth longer than the dentigerous arm) and have a slight but obvious posterior

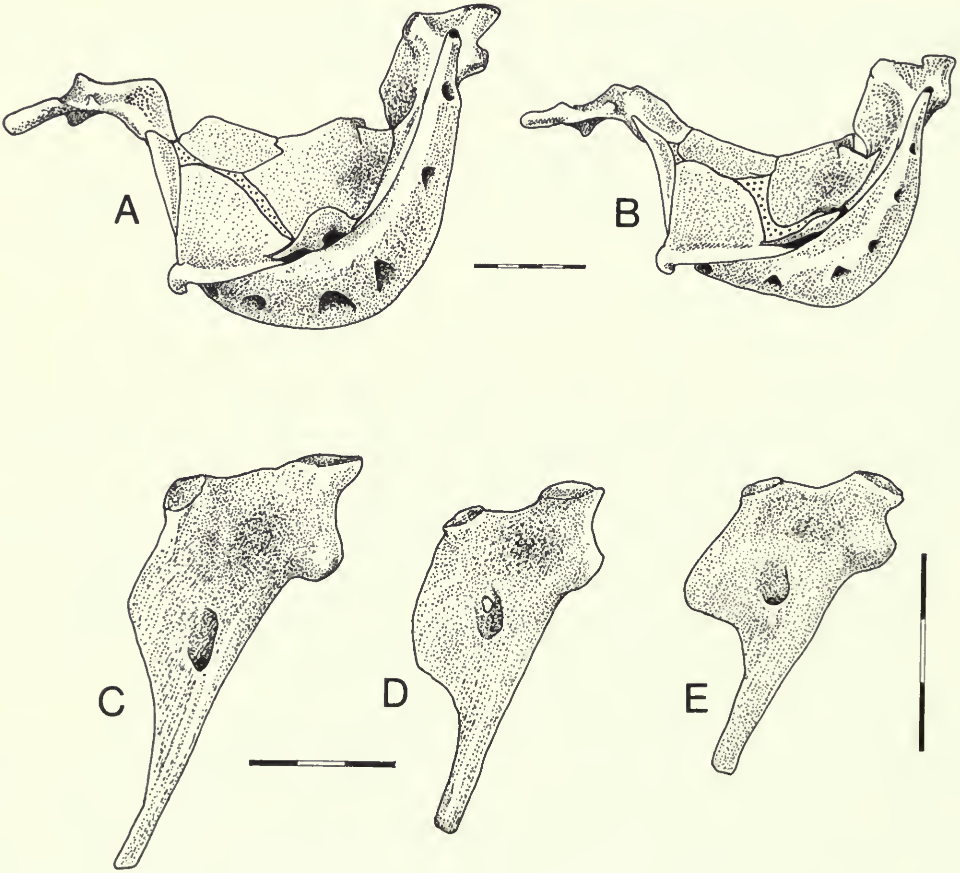

Fig. 3 A, Suspensorium of *Thoracochromis buysi*; B, that of *Th. albolabris*, both in left lateral view. C, D & E, hyomandibula, in left lateral view, of C, *Th. buysi*; D, *Th. albolabris*; E, *Orthochromis machadoi*. Scale in mm.

inclination at an angle of about 10° from the vertical. The dentigerous arms are laterally compressed and are not expanded anteriorly and anteroventrally to form a beak-like process.

Caudal fin skeleton. All the hypurals are free in 22 of the specimens radiographed but in some hypurals 3 and 4 are very closely apposed to one another, and in two others hypurals 1 and 2 are fused. In another fish, hypurals 1 and 2 seemingly are fused distally but are free proximally, as are hypurals 3 and 4. All these observations were made from radiographs thus rendering it difficult to distinguish with certainty between actual fusion and close apposition.

Vertebrae. Excluding the fused PU_1+U_1 centra, there are 30 (f8), 31 (f10), 32 (f4) or 33 (f1) vertebrae, comprising 13 (f2) or 14 (f21) abdominal and 16 (f7), 17 (f10), 18 (f5) or 19 (f1) caudal elements.

The syntypical specimens of *Tilapia steindachneri,* from the Que river, are excluded from these counts; here the range is 28 (f1), 29 (f1) and 31 (f3), comprising 12 (f1), 13 (f1) or 14 (f3) abdominal, and 15 (f1) or 17 (f4) caudal centra.

In her original description of *Th. buysi,* Penrith (1970: 169) gives the vertebral count (including PU_1+U_1) for the holotype as 16+18; I have checked this figure on a radiograph made in the BM(NH), and find that my count, including the PU_1+U_1 elements, is 14+18.

Coloration. No information is available on live colours. For material fixed in formol and preserved in alcohol, the coloration is: *Females and immature males,* with a light brown (beige) ground colour which often becomes silvery on the belly and the flanks below the midlateral line. The intensity and presence of the silvery pigment may depend on factors of preservation since in some specimens it is absent, the beige colour merely lightening on the lower half of the belly. In those specimens which are silvery, faint traces of silver are present on the cheek and, more intensely, on the operculum. Traces of from 8–12 vertical bars are visible on the flanks and caudal peduncle; some of these bars extend almost to the ventral body profile, but most fade and disappear slightly below the level of the midlateral line. The intensity and clarity of the bars is very variable in the sample as a whole, but are reasonably constant within any one sample. Dr Michael Penrith (*in litt*) has observed, for the small cichlids of the Cunene, that coloration is generally darkest in fishes from the upper reaches of the river.

All fins are greyish-hyaline, the *dorsal* with darker pigmentation between the spines, and dark maculae between the branched rays; the lappets are darker than the areas between the spines. The *caudal* fin is faintly maculate, with a dark posterior margin; this marginal band is most obvious when the fin is closed. The *anal* has dark lappets, and some indication of a dark margin to the anterior region of the soft part as well. In some males there are 5 or 6 dark spots, arranged, somewhat irregularly, in two rows on the soft part of the fin; the distal row lies a little above the fin's margin, the proximal row (usually with fewer spots) lies along the middle of the fin. There is no indication of a clear surround encompassing each of the spots, which thus cannot be considered true ocelli. The *pelvic* fins sometimes have a peppering of dark chromatophores which are most obvious in males.

Sexually active males. In the few sexually active males examined, the overall coloration is much darker than that in females and inactive males. Scales above the midlateral line are outlined in dark brown, the vertical barring is moderately intense, the dorsum of the head and the entire snout is dark, almost dusky, as are the rami of the lower jaw and the anterior two-thirds of the lower lip. The branchiostegal membrane and the chest are dusky, but are lighter than the dentaries. The cheek is brown and only a little darker than the ground colour of the body.

The membrane between the *dorsal fin* spines is almost black, but the lappets are hyaline; the soft part of the fin is densely maculate, the spots having a clear centre and a narrow, very dark brown surround. The proximal two-thirds of the *caudal fin* is covered in similar maculae, but its distal third is a somewhat dusky hyaline; the posterior margin is dark. The *anal fin* has a dusky hyaline ground colour showing between the large number, 8–10, of pale spots, each with a narrow, dark surround. The spots are arranged in three irregular rows (with from one to three spots in each) on the soft part of the fin. The anal spots are about four times larger than the biggest maculae occurring posteriorly on the dorsal fin. The *pelvic fins* are very dusky, almost black over the proximal half of each fin. The *pectorals* are hyaline.

DISTRIBUTION. *Thoracochromis buysi* is known only from the Cunene river, including one of its tributaries, the Que.

DIAGNOSIS AND AFFINITIES. Within the genus *Thoracochromis*, this species would seem, at least anatomically, to be a relatively primitive member of the group. This is particularly so when comparisons are made with species from the Nile and Lake Turkana (see Greenwood, 1979: 293–4). Unfortunately, insufficient information is available for many species occurring in Lake Mweru and the Zaire system to indicate what level of relationship might exist between them and *Th. buysi*. What information we have, however, does not suggest that a sister-species relationship is likely.

In their overall appearance and most anatomical characters, two of the other Angolan *Thoracochromis* species, *Th. schwetzi* and *Th. lucullae*, are very similar to *Th. buysi*. Neither species occurs in the Cunene river, and only *Th. schwetzi* is well-represented by numerous specimens.

Thoracochromis buysi differs from *Th. lucullae* mainly in having the depth of the preorbital bone greater, and not less than, the interorbital width (or, rarely, equal to it), and in details of its dentition. In *Th. lucullae*, the outer row jaw teeth have a relatively larger and broader minor cusp, with the result that its teeth are less unequally bicuspid than are those in *Th. buysi*. There are indications from the few available specimens of *Th. lucullae* that the scales are larger than in *Th. buysi*; there are 32 lateral-line scales in *Th. lucullae* as compared with a modal count of 34 or 35, rarely 32 or 36, in *Th. buysi*, and the cheek scale rows are generally more numerous in *Th. buysi* (3–5, mode 4, *cf* 3 in *Th. lucullae*). Neurocranial form, and the osteological features of the jaws, are similar in the two species, although the narrower interorbital region in the skull of *Th. buysi* is very obvious. The suspensorium is damaged in the only skeleton of *Th. lucullae*, so it is impossible to check whether or not that species has a palatopterygoid gap (see p. 194 above).

Thoracochromis buysi is also very similar to *Th. schwetzi*, which differs, however, in having unicuspid jaw teeth in specimens of a much smaller size. It also differs in generally having only a single series of inner teeth anterolaterally in both jaws, compared with the modal condition of 2 or 3 rows in *Th. buysi*. Like *Th. lucullae*, *Th. schwetzi* has a shallower preorbital bone than *Th. buysi* (15·8–20·0% head length, *cf* 18·5–26·0, M = 22·9% in *Th. buysi*) the depth of which is always less than the least interorbital width.

In all three species the basic shape of the bicuspid outer row jaw teeth is similar, as is that of the tricuspid inner teeth. The unicuspid outer teeth in *Th. schwetzi*, however, are more slender and cylindrical in cross-section than are the unicuspids occurring in the other two species.

The overall similarity of these three species, each from a different river system, might suggest that each is the vicariant (*i.e.* replacement) sister-species of the others. However, it must be stressed that there are as yet no synapomorphic characters known to be uniquely shared by the three taxa, and so their possible sister-species relationship cannot be established unequivocally.

Thoracochromis buysi differs from *Th. albolabris*, the fourth Angolan member of the genus, in several characters, all of which are autapomorphic for *Th. albolabris*. The most obvious of these are the greatly thickened, often lobate lips of *Th. albolabris*, the very small chest scales in that species, and its narrower, near V-shaped dental arcades (see p. 201).

Regrettably, I have not been able to examine the holotype of Steindachner's species '*acuticeps*', whose generic status thus remains unknown. It is clear from Penrith's (1970: 171) comments, and from Dr Trewavas' personal examination of the *acuticeps* type specimen, that *Th. buysi* differs from it in several features. In particular, *Th. buysi* has a less massive lower pharyngeal bone with smaller median pharyngeal teeth, and its lower jaw is shorter than in '*acuticeps*'.

The precise locality from which the type of '*acuticeps*' was collected is unknown, and no descriptions of additional material have ever been published, apart, that is, from Regan's (1922) account which is clearly based on a polyspecific sample (see Trewavas, 1973: 31, and personal observations).

Study material and distribution records

Registered material

Museum register number		Locality
Staatsmuseum Windhoek 5099 (Holotype)		Cunene river mouth
SAM 25243 (paratype)		Cunene river mouth
BMNH; P = collection number:		
1984.2.6:1–7	P1682	Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:8	P1347	Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:9–14	P1403	Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:15–18	P1422	Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:19–23	P589	Cunene R., below Ruacana falls (17° 24′S, 14° 13′E).
1984.2.6:24	P89	
1984.2.6:25–27	P121	Cunene R., 3 miles west of Swartbooisdrif. (17° 19′S, 16° 58′E).
1984.2.6:28–38	P1780	Foz do Cunene (17° 15′S, 11° 43′E).
1984.2.6:39–52	P1781	Foz do Cunene (17° 15′S, 11° 43′E).
1984.2.6:53	P1841	Cunene R., Otjinungwa (17° 12′S, 12° 20′E).
1984.2.6:54	P1126	Cunene R., Matala Dam, Luceque (14° 36′S, 15° 18′E).
1984.2.6:55–56	P1128	Cunene R., Matala Dam, Luceque (14° 36′S, 15° 18′E).
1984.2.6:57–62	P1157	Cunene R., Chitapua (14° 23′S, 15° 18′E).
1984.2.6:63	P1186	Cunene R., Jamba-ia-Homa (13° 46′S, 15° 30′E).

Unregistered material

Locality	Number of specimens	Collection no.
Cunene R., 10 miles west of Ruacana (17° 26′S, 14° 05′E).	2	P611
Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).	1	P1416
Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).	4	P1347
Foz do Cunene (17° 15′S, 11° 43′E).	10	—
Cunene R., Otjinungwa (17° 12′S, 12° 20′E).	1	P1324
Cunene R., Otjinungwa (17° 12′S, 12° 20′E).	1	P1325
Cunene R., above Epupa falls (17° 00′S, 13° 15′E)	1	P696
Cunene R., near Cafu (16° 30′S, 15° 10′E).	1	P808
Cunene R., 82 km west of Ondurusu falls (15° 59′S, 13° 22′E).	5	P1289
Cunene R., Chitapu (14° 23′S, 15° 18′E).	3	P1116
Cunene R., Chitapu (14° 23′S, 15° 18′E).	1	P1176

Thoracochromis albolabris (Trewavas & Thys van den Audenaerde), 1969

SYNONYMY. *Haplochromis albolabris* Trewavas & Thys van den Audenaerde, 1969. *Mitt. zool. St Inst. Hamb.* **66**: 237–239, figs 1 & 2, plate 13.

DESCRIPTION. Based on 18 specimens, *ca* 30–121·0 mm SL. Since 11 of these specimens were badly distorted before or during preservation, morphometric features are taken from 7 individuals only, 37·0–121·0 mm SL; these include the holo- and paratype of the species. Information on dentition, lip form and various meristic characters are, however, supplemented by data taken from the distorted specimens. Because the sample size from which the morphometric characters are derived is so small, ranges but not means or modes are given for those features.

Depth of body 29·7–34·5% of standard length, length of head 32·0–36·7%.

Dorsal head profile straight or very gently curved, sloping at an angle of 30°–35° to the horizontal, its outline sometimes interrupted by the slight prominence of the premaxillary ascending processes. The upper margin of the orbit lies distinctly below the outline of the head.

Preorbital depth 16·0–22·4% of head length, least interorbital width 16·0–21·4%. Preorbital depth and interorbital width are equal in 2 specimens, the preorbital depth is greater in 4 others, and the interorbital width is greater in one specimen (see p. 191 above).

Snout length 36·0–44·0% of head length and 1·3–1·6 times its breadth; in one exceptional specimen the length-breadth ratio is 1·9.

Eye diameter 25·0–32·0% of head length, the largest eye being that in the smallest specimen measured (37·0 mm SL). Cheek depth is 19·6–24·2% of head length.

The caudal peduncle is 1·3–1·7 times longer than deep, its length 17·0–19·3% of standard length.

With such a small sample it is impossible to detect any features which might vary allometrically with standard length. The highest percentage ratios for preorbital depth, interorbital width, and pectoral fin length (see below) are, however, those for the smallest individual measured.

The lips exhibit a wide but continuous variation in form, from those (as in the type specimens) which are clearly much thickened, but uniformly so (Fig. 4), those which are not only thickened but are produced medially into prominent lobes (Fig. 5). This latter condition is identical with that occurring in extreme individuals of *Lobochilotes labiatus* (Lake Tanganyika) and *Paralabidochromis chilotes* (Lake Victoria) and in the one *Melanochromis labrosus* (Lake Malawi) available for study. The intermediate stages of lip development seen in *Th. albolabris* are also encountered in the first two species listed above; *M. labrosus* is known from too few specimens to allow comment on that point.

The degree of lip development in *Th. albolabris,* at least with respect to lobe formation, is not obviously size correlated; uniformly and distinctly thickened lips are present in

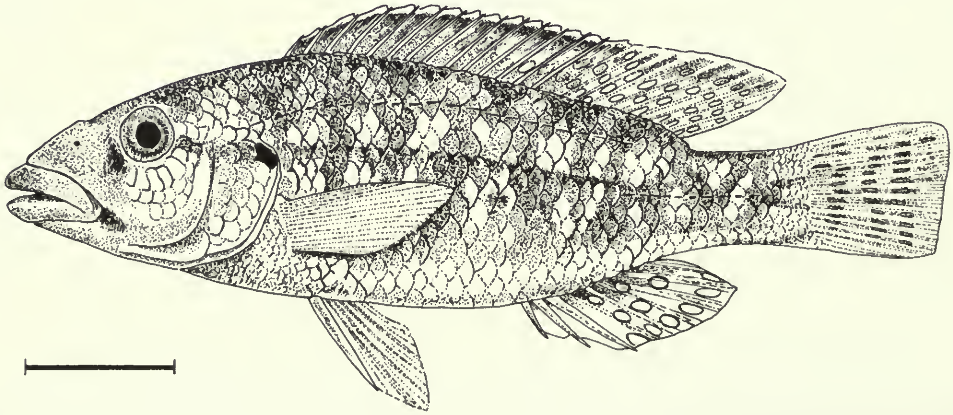

Fig. 4 *Thoracochromis albolabris*; after Trewavas & Thys van den Audenaerde (1969). Drawn by G. J. Howes. Scale = 20 mm.

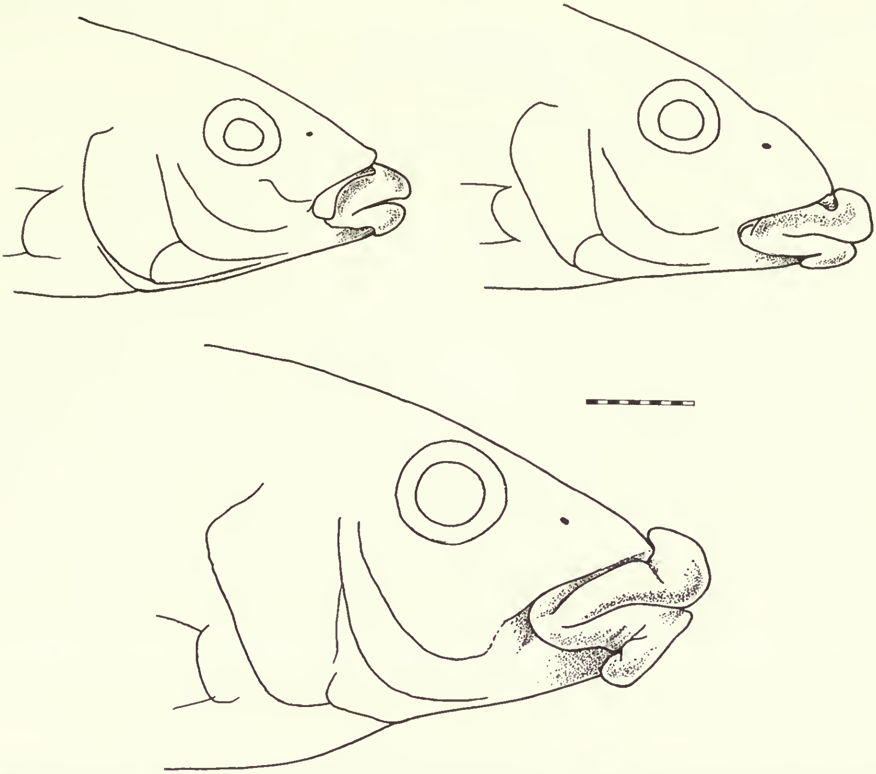

Fig. 5 *Thoracochromis albolabris.* Variations in lip and lobe development. Scale in mm.

specimens throughout the size range available. Some large specimens, for example the holotype 96 mm SL and the paratype 121 mm SL, have unlobed lips; incipient lobes are present in some specimens 33–76 mm SL, and moderate lobes are developed in a fish 77 mm long. Other individuals in the size range 30–40 mm show no trace of lobes, but the lips are developed to an extent comparable with those in the much larger type specimens. Fully developed lobes are found in fishes of 73, 92, 93 and 121 mm SL.

Because some large specimens lack lobes it is impossible to determine whether or not small specimens without lobes are at an early stage of future lobe development. But, judging from the sample studied it seems probable that lobes are not well-developed in fishes of less than 45–50 mm standard length.

Since considerable variation in the extent of lobe development is recorded for other cichlid species (see Greenwood, 1981 for the Lake Victoria species), I have no doubt that this sample of Cunene fishes is conspecific, particularly since all share other, and uniquely derived features as well.

The mouth is horizontal or nearly so, the posterior tip of the maxilla either reaching a vertical passing close to the anterior orbital margin, or one lying about midway between it and the nostril.

The ascending processes of the premaxilla are 34·5–41·0% of head length, the length of the lower jaw 35·2–40·0% and its length-breadth ratio is 1·3–1·7.

Gill-rakers and pharynx. There are 11 (f1), 12 (f3), 13 (f3), 14 (f3), 15 (f4) or 17 (f1) rakers in the outer row on the lower part of the first gill-arch; one specimen has 9 rakers on one side and 11 on the other. Except for the lower 4 or 5 elements, the rakers are short and stout to moderately stout, transversely elongate, and with the upper surface generally thrown into 2 or 3 cusps. The lower 4 or 5 rakers are reduced to little more than low knobs; the size-range of the lower rakers is positively correlated with the length of the fish, being barely visible in specimens less than 35 mm SL.

The microbranchiospines are sometimes difficult to detect, but although small are always present.

As in *Th. buysi*, the dorsal epithelium of the pharynx is thickened, noticeably corrugated and papillose. The prepharyngeal pads are well-developed and are like those of *Th. buysi* in size and shape.

Scales are weakly ctenoid on the flanks below the upper lateral-line, and are very weakly ctenoid to cycloid on the caudal peduncle and above the upper lateral-line on the flanks. In larger specimens the degree of ctenoidy is weaker than in smaller individuals.

The size-transition between the scales on the chest and those on the ventrolateral aspects of the flanks is abrupt; the chest scales are very small and deeply embedded. Two specimens appear to have small naked areas ventrolaterally on the chest, but closer examination shows that the scales in these areas are more deeply embedded than elsewhere in the region.

There are 32 (f1), 33 (f7), 34 (f5) or 35 (f3) scales in the lateral-line series, 4½ to 6½ (generally 5 or 5½) between the dorsal fin origin and the upper lateral-line, and 8 to 10 between the pectoral and pelvic fin insertions. The cheek has 3 to 5 scale rows (usually 3), generally embedded deeply in the thickened skin. Anteroventrally there is a distinct but sometimes small naked embayment, and there is always a narrow naked strip between the cheek scales and the preoperculum.

With one exception, all specimens have one large and one small scale between each of the last 4 or 5 scales in the upper lateral-line and the dorsal fin base. In the exceptional fish there are, on one side, two large scales between the lateral-line and the fin, and on the other side two large and one small scale.

Fins. Dorsal with 14 (f1), 15 (f14) or 16 (f1) spinous and 10 (f2), 11 (f9) or 12 (f5) branched rays, the anal with 3 spinous and 7 (f4), 8 (f10) or 9 (f1) branched elements.

All but three fishes (30–35 mm SL) have either a well-developed scale sheath at the base of the anal, or isolated sheath scales present in that region, even in specimens as small as 33–34 mm SL.

The pectoral fin is 18·9–25·0% standard length, 56·0–66·8% of head length. The pelvic fins have the first branched ray only a little longer than the second, or rarely, the two are of equal length. In large adult males, however, the first ray is clearly longer than the second, but is not drawn out into a distally filamentous projection.

The caudal fin is subtruncate and is scaled over its proximal third to half, or exceptionally, over its proximal two-thirds.

Teeth. The dental arcade in *Th. albolabris* (Fig. 6) is more nearly 'V'- than 'U' shaped, especially in specimens with fully lobate lips. A similar correlation of arcade shape with lip development is seen in other species, mentioned above, with lobed lips (Greenwood, 1959: 209, and other observations).

The *outer teeth* (Fig. 2B), in virtually all the specimens have worn cusps, thus making it difficult to describe accurately the form of the crown. Unworn teeth in fishes over 75 mm SL are either unicuspid or weakly bicuspid; in bicuspids the minor cusp, although reduced as compared with that cusp in *Th. buysi,* does show a similar angling away from the major cusp. Fishes in this size range generally have unicuspid teeth posteriorly in the premaxillary series. As in *Th. buysi*, these and other unicuspids are slender and relatively compressed, with attenuated rather than pointed crowns; that is, they could not be described as caniniform.

From the sample available it seems that in fishes less than 75 mm SL the majority of unworn teeth are distinctly but unequally bicuspid, with a cusp shape and arrangement like that in the weakly bicuspid teeth of larger individuals. Teeth situated posteriorly in the outer premaxillary row of these smaller fishes are weakly bicuspid.

There are 22–64 teeth in the outer premaxillary series, the number probably having a positive correlation with standard length, although in one of the largest specimens (121 mm SL) there are only 50 teeth, and a specimen of 37 mm has 60.

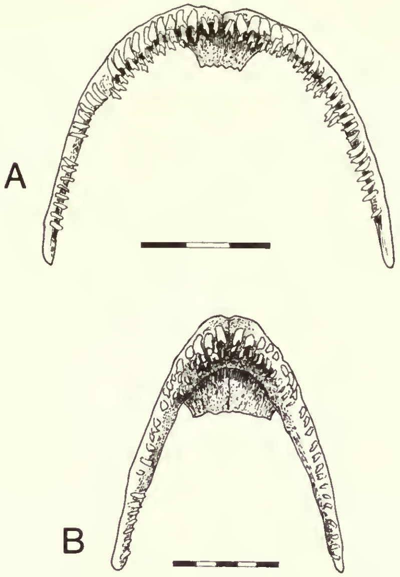

Fig. 6 Premaxilla, in occlusal view, of: A, *Thoracochromis buysi*; B, *Th. albolabris* to show difference in outline of dental arcade; only the basal region of the ascending processes is shown. Scales in mm.

The *inner teeth* are arranged, anteriorly and laterally, in from 1 to 4, usually 2, rows in the upper jaw, and in 1 to 3, usually 2, in the lower jaw; posterolaterally in both jaws only a single row is present.

Fishes less than 70 mm SL have mostly weakly tricuspid inner teeth in which the larger median cusp is flanked by slight, shoulder-like projections. Fishes over 70 mm SL may have an admixture of tri- and weakly bicuspid teeth or of bi- and, predominantly, weakly bicuspids, or most of the teeth may be unicuspids.

Lower pharyngeal bone and dentition (Fig. 7B). The anterior shaft is short, the dentigerous area triangular and varying from slightly longer than broad, through equilateral, to slightly broader than long. Some variation exists in the stoutness of the bone. In the holotype it is moderately stout, the stoutest seen amongst the specimens available. In other, and larger, fishes the bone is but slightly thickened, while in the majority of specimens it shows no marked departure from the generalized condition seen in *Th. buysi*.

There is variation, too, in the degree to which teeth in the median pair of tooth rows are enlarged or coarsened. Certain of the larger specimens (including the holotype) have some of these teeth distinctly enlarged with near-molariform crowns, but in the majority of specimens the teeth are slender and cuspidate, those situated in the posterolateral corners of the dental field being more closely spaced than elsewhere.

Osteology. The neurocranium is similar to that of *Th. buysi* (Fig. 10B) in its general form, but has a lower supraoccipital crest, a flatter (that is, less concave) interorbital skull roof, and a convex not concave surface to the posterior part of the roof contributed by the frontals. The apophysis for the upper pharyngeal bones is of the *Haplochromis* type, but in some specimens the basioccipital contribution to the facet is rather small (although never as small as in the *Tropheus* type of apophysis; see Greenwood, 1978).

Expressed as percentages of neurocranial length (18·5 mm in the one skull available for measurement) the orbital depth is 37·9%, the preorbital depth 23·3%, the ethmovomerine

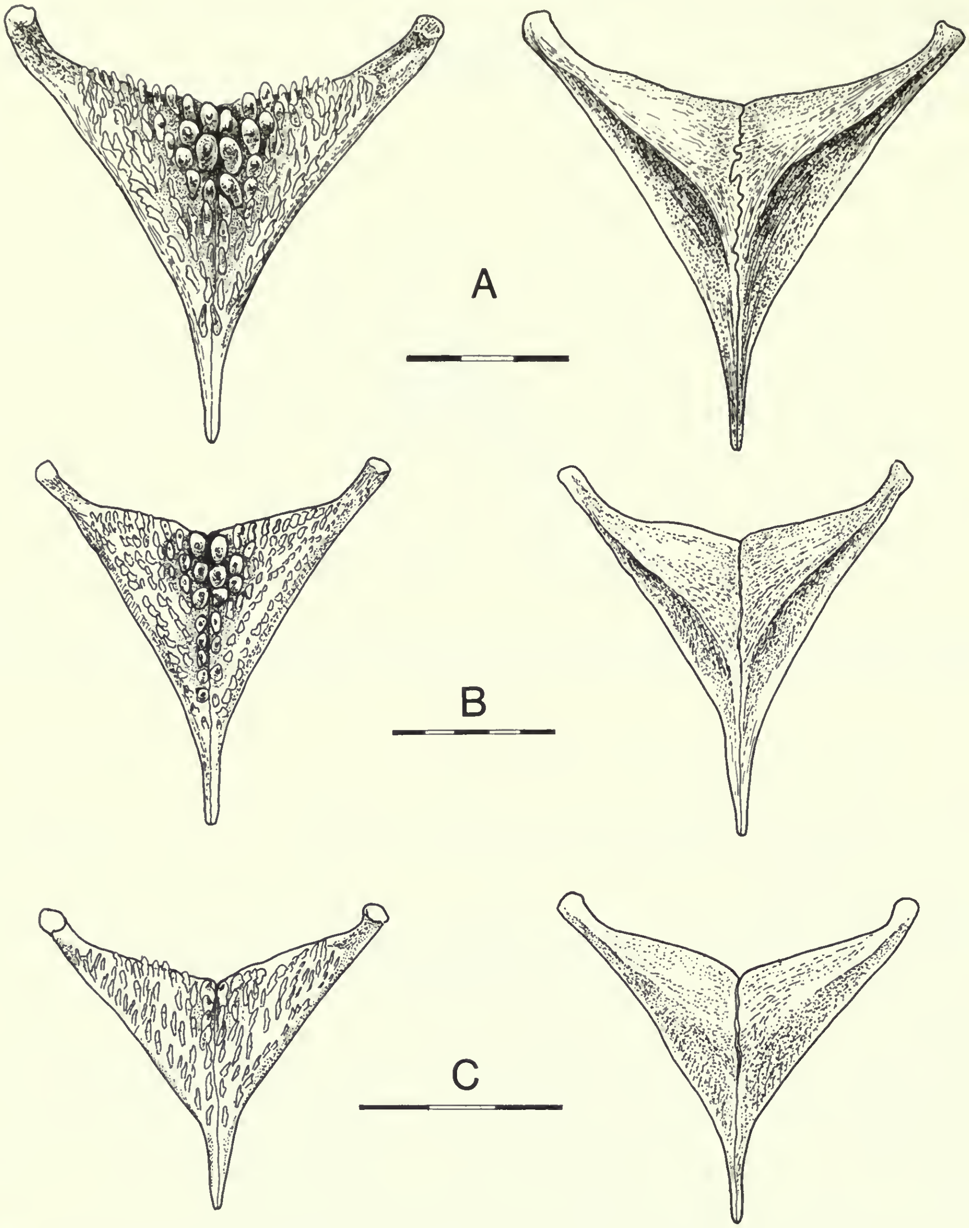

Fig. 7 Lower pharyngeal bones, in occlusal and ventral views, of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Scale in mm.

length 28;7%, the depth of the otic region 39·9%, the width of the otic region 51·3%, and the greatest height of the supraoccipital crest 13·5%.

Suspensorium. Unlike that in *Th. buysi,* the suspensorium in *Th. albolabris* (Fig. 3B) has no gap between the palatine and entopterygoid bones, and the posterior margin of the palatine is gently curved rather than rectangular. The anterior flange on the hyomandibula in *Th. albolabris* is slightly more expansive than in *Th. buysi.*

Jaws. Relative to that in *Th. buysi,* the maxilla in *Th. albolabris* is foreshortened (Fig. 8D & E). The *premaxilla* (Fig. 8B) has elongate ascending processes which are about 1·25

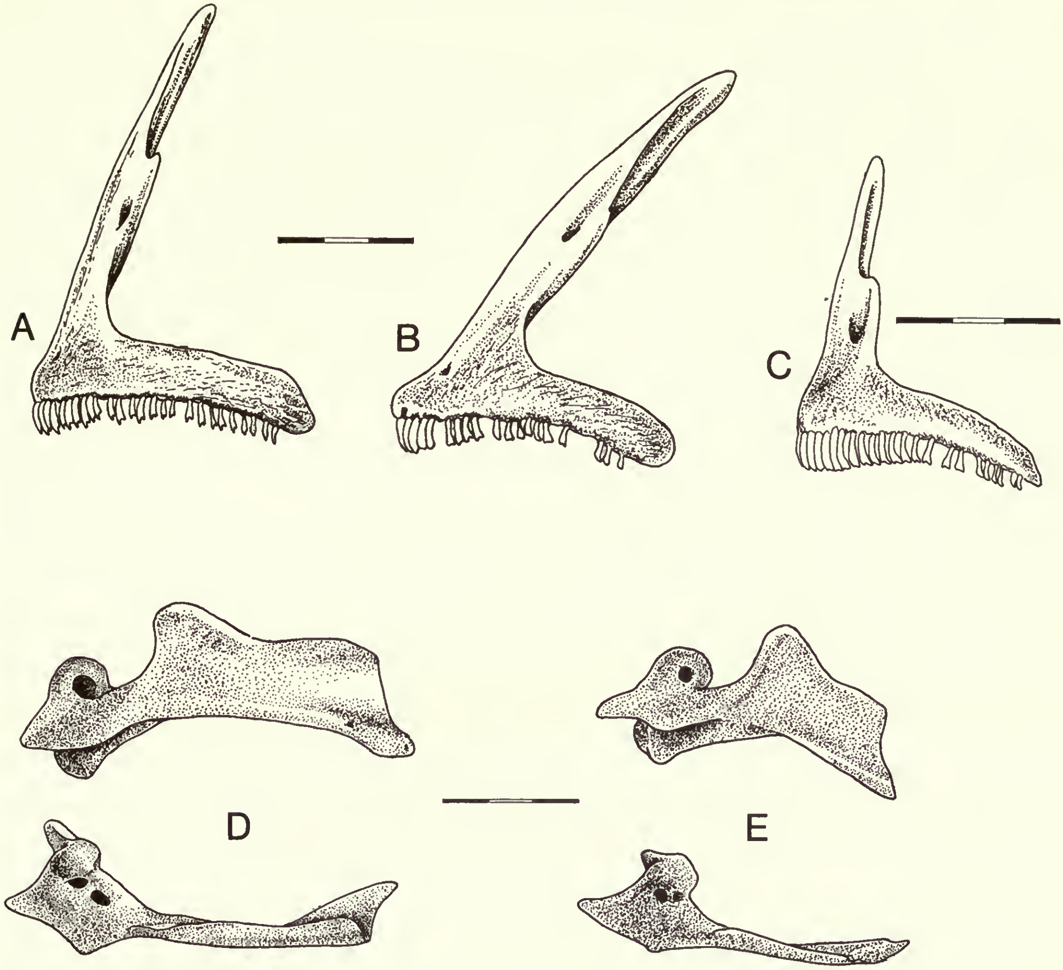

Fig. 8 Premaxilla (upper row) of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Maxilla, in left lateral and dorsal view (middle and lower rows respectively) of: D, *Th. buysi*; E, *Th. albolabris*. Scale in mm.

times the length of the dentigerous arms, and which slope strongly backwards at an angle of about 25° to the vertical. In occlusal view the two dentigerous arms are arranged so as to form a 'V'-rather than a 'U'-shaped outline (Fig. 6). These arms are not inflated, but anteriorly and somewhat anteroventrally each is produced forward beyond the base of the ascending process to form a prominent, shelf-like beak (Fig. 8B). The dentary (Fig. 11B) is like that in *Th. buysi,* but the rami of each side meet to form a more nearly 'V'-shaped occlusal surface in *Th. albolabris,* and the anterior 'shelf' is more prominent.

Caudal fin skeleton. All five hypurals are separate from one another in six of the nine specimens examined (1 alizarin specimen and 8 radiographs), but in the three others, hypurals 3 and 4 are so closely apposed as to appear almost fused.

Vertebrae. Excluding the fused PU_1 and U_1 centra, there are 30 (f2) or 31 (f5) vertebrae, comprising 13 (f1) or 14 (f6) abdominal and 16 (f2), 17 (4) or 18 (f1) caudal elements.

Coloration. Live colours are unknown, and the coloration can only be described for formol fixed and alcohol preserved specimens.

There are no sexually active fishes in the entire sample available for study. *Immature and sexually quiescent individuals of both sexes* have a similar coloration. The ground colour is light brown (beige), darkening to greyish-beige on the dorsum of the head in some individuals. The body is crossed by 7–10 bars, often of irregular outline and shape, and either vertically or somewhat obliquely aligned. Some may be simple bars, others are narrowly triangular with, in any one specimen, the apex directed either dorsally or ventrally. Several specimens have a faint and narrow midlateral stripe extending the whole length of the body; a second narrow band runs along the upper lateral-line scale row, interconnecting the bars over the posterior half of the body. In some specimens there is a rather broad but faint lachrymal stripe running from the anteroventral margin of the orbit to the angle of the jaw; others have, in addition, a narrow bar across the snout between the anterodorsal margins of the orbits.

All the fins are hyaline, the spinous *dorsal* with dark streaks between the rays, and dark lappets; the soft dorsal is fairly densely maculate, the maculae either solid, or light-centred with a ring of dark marginal spots circumferentially. The *caudal* is densely and darkly maculate over most of its length, with, in at least some individuals, a dark posterior margin. In one of the males examined there are numerous light-centered but dark margined spots arranged rather irregularly in two or three rows; none of the spots has a clear surround. Other males, and most females, have the anal fin hyaline, but in some almost the anterior half of the anal fin is a light greyish-sooty colour. The *pectoral* and *pelvic* fins are hyaline, but in one male there are faint dusky areas over about the anterior third of the pelvic fins.

The figure of the holotype, a male, published by Trewavas and Thys van den Audenaerde (1969: plate 1) gives a good impression of a darkly pigmented fish; the specimen, however, is now somewhat faded.

DISTRIBUTION. Known only from the Cunene river, see also p. 205.

DIAGNOSIS AND AFFINITIES. Specimens of *Th. albolabris* with lobed lips are immediately distinguishable from all other cichlids occurring in the Cunene river. Those specimens without obvious lobes are recognisable by the degree to which the lips are thickened and by the near 'V'-shaped dental arcade, both features which, of course, also serve to diagnose lobe-lipped individuals as well.

Thoracochromis albolabris is further distinguished from all Cunene haplochromines, except *Orthochromis machadoi* (see p. 206), by the very small size of its chest scales, and from all, except the species of *Serranochromis*, by its high gill-raker counts (11–17). From the *Serranochromis* species it is distinguished by various dental characters and several morphometric features as well.

From *Orthochromis machadoi, Th. albolabris* is distinguished by its head shape, dental pattern, absence of naked areas on the chest, and by having the first branched pelvic ray at least equal in length to the second ray, and generally a little longer than it.

When first describing *Th. albolabris*, Trewavas and Thys van den Audenaerde (1969) compared the taxon with a then undescribed haplochromine which they considered to be '. . . very close to our species'. The undescribed species was *Th. buysi*, from which *Th. albolabris* can be separated readily on the several features noted above, particularly the high gill-raker count. The two taxa do share certain features, for example, a similar tooth morphology and various meristic and morphometric similarities, but none can be considered as synapomorphies indicative of a sister-species relationship between these species. Indeed, the resemblances are all in plesiomorph characters.

When compared with the *Thoracochromis* species occurring in other parts of Africa (Greenwood, 1979), *Th. albolabris* does exhibit a large number of derived features, for example, the hypertrophy of its lips, the high gill-raker count, the beaked premaxilla with its strongly angled ascending process, and the near 'V'-shaped dental arcade. Again, none of these features is an intrageneric synapomorphy; as autapomorphies, none can be used to

Study material and distribution records

Museum register number		Locality
ZMH 1784 (Holotype)		Cunene R., Matala (14° 43′S, 15° 04′E)
Stockholm Museum, NRM NNN/951989, 7151		Southern Angola; locality unknown. Collected by M. Fröhlich.
BMNH;	P=collection no.	
1972.9.27:89		Cunene R., above Epupa falls (17° 00′S, 13° 15′E).
1984.2.6:101	P710	Cunene R., 1 mile east of Epupa falls (17° 00′S, 13° 15′E).
1984.2.6:87–89	P1483	Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:90	P609	Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:91	P1276	Cunene R., 32 km west of Odurusu falls (17° 15′S, 13° 42′E).
1984.2.6:92–98	P1389 (one an alizarin prep.)	Cunene R., 54 km west of Ondurusu falls.
1984.2.26:99–100	P643 (one used for skeletal prep.)	Cunene R., 27 miles west of Ondurusu falls (17° 10′S, 13° 33′E).

establish the intrageneric relationships of *Th. albolabris*. That *Th. albolabris* shows such a high number of derived features would seem to negate the views of Trewavas and Thys van den Audenaerde (1969: 238), who considered that it should be ranked amongst the generalised haplochromines. For the moment, *Th. albolabris* must remain a phylogenetic isolate amongst its congeners.

In the hyperdevelopment of its lips, and in other, possibly correlated characters, *Thoracochromis albolabris* resembles *Paralabidochromis chilotes* of Lake Victoria, *Cyrtocara lobochilus* and *C. euchilus* (Lake Malawi), *Melanochromis labrosus* (Lake Malawi) and *Lobochilotes labiatus* (Lake Tanganyika). In each of these lakes there are other species, too, some still undescribed, which resemble *Th. albolabris* in having hypertrophied lips as well as sharing certain dental and osteological features with that taxon.

I have made detailed comparisons of *Th. albolabris* with all these species, and find that on the basis of various characters and character combinations, arguments can be deduced which would militate against postulating *Th. albolabris* as having a close phylogenetic relationship with any but one of them, namely *Melanochromis labrosus*. For example, the dentition and the morphology of the jaws, together with details of the neurocranial osteology in *Lobochilotes labiatus, Cyrtocara euchilus* and *Paralabidochromis chilotes* differ quite trenchantly from the condition seen in *Th. albolabris,* and in the two latter species there are differences in squamation patterns as well. Few anatomical details could be studied in *Cyrtocara euchilus*, a species represented in the BMNH collections only by the type specimen. It differs from *Th. albolabris* in having an *Astatotilapia*-type of chest squamation (see Greenwood, 1979: 270; fig. 1), and there also appear to be differences in the dental morphology of the two species.

On the basis of their sharing the greatest number of derived features, the Malawian *Melanochromis labrosus* would thus seem to be the species most closely related to *Th. albolabris*. Unfortunately, as *M. labrosus* is known only from one specimen, its osteology could not be studied in any detail. For that and other reasons, especially our great ignorance of cichlid interrelationships in general, I would not develop any further the suggestion that *Thoracochromis* and *Melanochromis labrosus* might be closely related.

ORTHOCHROMIS Greenwood, 1954

This genus, originally defined on the basis of one species, *Orthochromis malagaraziensis* (David), was later expanded to include three other taxa (see Greenwood, 1979: 295–7). At that time the Cunene river species, *O. machadoi* (Poll), was known only from the two types and one other specimen.

The greatly increased number of *O. machadoi* specimens now available for study requires that two of the diagnostic features for the genus be modified. In my 1979 paper (page 296) it was indicated that all the upper lateral-line pore-bearing scales in *Orthochromis* are each separated from the dorsal fin base by not more than one large and one much smaller scale. (The few anterior scales in the upwardly curving portion of the lateral-line are excluded from that generalization.) In *O. machadoi*, however, only the last 9–12 pored scales of the upper lateral-line are separated from the fin in this way, the more anterior scales having two large scales between them and the fin base; in one specimen only the last 3–5 scales have less than two equal-sized scales in that position. Apart from this exceptional specimen the number of lateral-line scales separated from the dorsal fin by less than two scales in *Orthochromis machadoi* is still high as compared with the usual condition in haplochromine genera, and represents a situation otherwise only found in *Ctenochromis* (see Greenwood, 1979: 287). Even here the modal number of lateral-line scales involved (8 or 9) is lower than in *O. machadoi.*

Although *O. machadoi* can be described as having a relatively elongate and slender body (see Greenwood, 1979: 296) its body depth is now known to range as high as 34·5% of standard length (*cf* the maximum of 30% cited in Greenwood, 1979), and the mean depth for the specimens sampled is 31·1% SL.

Apart from these modifications, no other data derived from the enhanced *O. machadoi* collection necessitates changes in the generic characters enumerated in Greenwood (1979). The additional material does, however, reinforce earlier conclusions that this species is the least derived member of the taxon (Greenwood, 1979: 298).

As far as I am aware, the new material also provides the first indication, in nature, that any species of *Orthocromis* is a female mouth-brooder (see Staeck, 1983: 178 for comments on the behaviour, in an aquarium, of an unidentified species resembling *O. polyacanthus*). A female *O. machadoi*, 40·5 mm SL, from Folgares (14° 55′S, 15° 06′E) is carrying fry in the buccal cavity. The characteristically distorted buccal cavity in some females from other localities also suggests that these fishes were carrying young at the time of their capture.

Orthochromis machadoi (Poll), 1967

SYNONYMY. *Haplochromis machadoi* Poll, 1967. *Publiçacões cult. Co. Diam Angola* no. 75: 313–315, fig. 152.

Orthochromis machadoi (Poll): Greenwood, 1979. *Bull. Br. Mus. nat. Hist.* (Zool.) **35**: 295–299.

DESCRIPTION. Based on 35 specimens, 38·0–65·0 mm SL, excluding the type and paratype which were examined previously (Greenwood, 1979). Various characters, such as squamation patterns, fin shape, body form, and dentition were checked on many other specimens, most of which were too distorted to use for morphometric purposes.

Depth of body 27·2–34·5 (M = 31·1)% of standard length, length of head 28·5–35·0 (M = 32·3%).

Dorsal head profile sloping upwards at an angle of 40°–50° to the horizontal, its outline not broken by the ascending premaxillary processes, and generally straight until a point above the middle of the orbits, after which it is gently curved; in some specimens the lower part of the profile is also slightly curved. The upper margin of the orbit lies distinctly below the level of the dorsal head profile.

Preorbital depth 13·7–29·9 (M = 18·2)% of head length; in one extreme individual the preorbital is only 12·5% of head length. Least interorbital width 12·5–20·0 (M = 16·0)% of

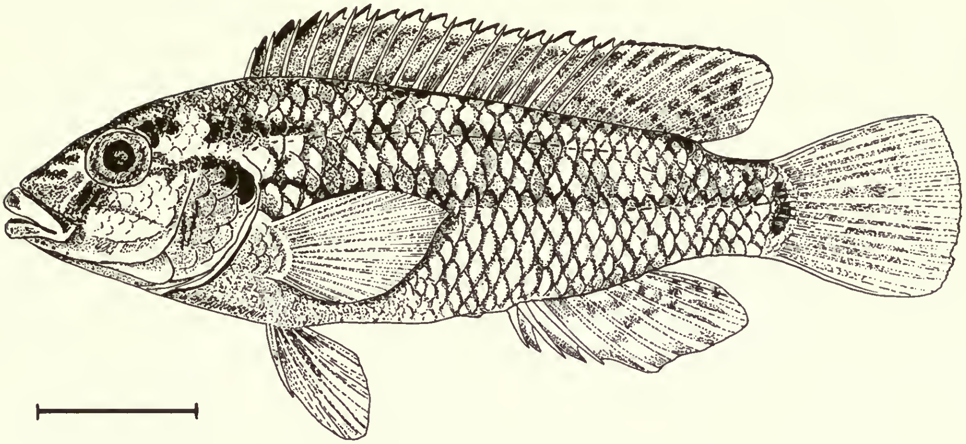

Fig. 9 *Orthochromis machadoi.* Drawn by G. J. Howes. Scale = 20 mm.

head, generally narrower than the preorbital is deep, but occasionally the measurements are equal.

Snout 0·8–1·1 times as long as it is broad (modally 1·0 times), its length 29·2–35·7 (M = 31·8)% of head.

Eye diameter 24·2–33·3 (M = 28·2)% of head, showing no obvious allometry with standard length. Cheek depth 20·8–33·3 (M = 25·4)%.

Caudal peduncle 1·2–1·5 times longer than deep (modally 1·4–1·5 times), its length 15·4–20·5% of standard length.

Mouth horizontal or almost so, the lower jaw generally a little shorter than the upper when the mouth is closed. Lips thickened (but not so noticeably as in *Th. albolabris*) with, in a few specimens, the dorsal margin of upper lip overlapping the ventral margin of the preorbital bone. The posterior tip of the maxilla reaches a vertical through the anterior margin of the orbit or, in a few specimens, extending either a little beyond, or not quite as far as that level. In the latter situation, however, the maxillary tip always reaches to a level well posterior to the nostril.

Lower jaw length 31·0–41·3 (M = 37·0)% of head, and 1·4–1·8 (mode 1·5) times its breadth. The length of the premaxillary ascending processes is 23·8–31·1 (M = 26·8)% of the head.

Gill-rakers and pharynx. There are 7 (f2), 8 (f17), 9 (f13) or 10 (f3) gill-rakers in the outer row of the lower part of the first gill-arch; the lower 1–3 rakers are reduced, the others short and stout, and not expanded transversely across the arch; the crown of each raker is simple or, less commonly, crenulate.

The prepharyngeal pads in *O. machadoi* are moderately developed and are comparable with those in the Cunene *Thoracochromis* species, but the pharyngeal epithelium is not noticeably thickened, neither is it distinctly papillate or thrown into longitudinal furrows. Well-developed microbranchiospines are present.

Scales. Above the upper lateral-line the scales are weakly ctenoid or cycloid, those below that level are ctenoid except for the cycloid scales on the chest and belly. The chest scales are very small and sharply demarcated in size from those on the ventrolateral aspects of the anterior flanks and belly. The ventromedial scales on the belly are markedly smaller than those on the ventral aspects of the flanks, and show an almost imperceptible size gradient with the scales on the chest (see Greenwood, 1979, fig. 3 for an illustration of the *Orthochromis* chest-belly squamation pattern; the belly scales in *O. machadoi* are relatively larger than those in the species depicted). Most specimens examined have, bilaterally, a naked area in the chest squamation. The size of this area shows some intraspecific variability, but in no specimen is the entire lateral region of the chest naked.

There are 29 (f1), 30 (f15), 31 (f12), 32 (f4) or 33 (f1) scales in the lateral-line series, $6\frac{1}{2}$–$8\frac{1}{2}$ between the upper lateral-line and the dorsal fin origin, 8–11 between the pectoral and pelvic fin bases, and 2–4 (modal range 2–3) rows on the cheek. Cheek squamation pattern is often irregular, but a horizontal naked strip is always present between the scale rows and the preoperculim, as is a small, anteroventrally situated, naked embayment of the scaled area.

There are never more than one large and one small scale between the dorsal fin base and each of the last 6–12 (modally 9–11) pored scales of the upper lateral-line; in one exceptional specimen, however, only the last 3 and 5 scales on the two sides respectively are separated from the fin in this manner, the other scales in the series being separated by 2 large scales of equal size.

Fins. Dorsal with 15 (f3), 16 (f20) or 17 (f10) spinous, and 9 (f8), 10 (f20) or 11 (f5) branched rays; anal with 3 (in one specimen 4) spinous and 7 (f1), 8 (f27) or 9 (f5) branched elements. In only 2 of the many specimens examined were traces of anal sheath scales observed (see p. 188), and then only as a single scale in each fish.

Caudal fin rounded or strongly subtruncate, scaled on its proximal half or, rarely, two-thirds.

Pelvic fins with the second branched ray longer than the first, and occasionally, the third also as long as the second; the pelvic spine and the first two rays of the fin are covered by greatly thickened skin.

Pectoral fin 18·3–23·9 (M=21·5)% of standard length, 57·0–81·3 (M=67·2)% of head length.

Teeth. In both jaws the *outer row* is composed of relatively slender, close-set and unequally bicuspid teeth (Fig. 2C). Generally from 1–3 slender unicuspids are situated posteriorly in the upper jaw. The number of teeth in the premaxillary outer row varies from 32–50 (modal range 46–50), the number showing weak positive correlation with the fish's standard length.

The *inner series* in both jaws are densely arranged in 2–4 (usually 3 or 4) rows anteriorly and anterolaterally, reducing to a single row posteriorly. The teeth are all tricuspid, with the median cusp slightly larger than the lateral ones.

Lower pharyngeal bone and dentition. The dentigerous surface is broader than long (*ca* 1·3 times), and the anterior shaft of the bone is short (Fig. 7C). Its teeth are cuspidate, fine and compressed, with only those in the posterior transverse row noticeably larger and coarser than the others. The teeth in the two median rows are barely coarser than those situated laterally.

Osteology. I have been able to compare, intragenerically, the skeleton of *Orthochromis machadoi* only with that of *O. malagaraziensis* (from the Malagarazi river, Tanzania). In all features which could be checked, the two species are virtually identical.

The *neurocranium* (Fig. 10C) is notable for its low supraoccipital crest, fairly steeply sloping (*ca* 45°) dorsal profile, gently rounded transverse profile of the skull roof anterior to the supraoccipital crest, and the slightly convex rather than concave camber to that part of the roof situated between the parietal crests and the base of the supraoccipital crest.

The apophysis for the upper pharyngeal bones is of the *Haplochromis*-type, with small but definite contributions from the basioccipitals.

Expressed as percentages of neurocranial length in the two 13 mm long skulls examined, the orbital depth is 38·0%, the preorbital depth 23·0%, the ethmovomerine length 30·8%, the depth of the otic region 46·0 and 48·5%, the width of the otic region 53·8%, and the height of the supraoccipital crest 15·4% (measured in only one skull).

Suspensorium (Fig. 3E). The palatopterygoid region is relatively foreshortened, and the hyomandibula has an expanded anterior flange which extends well beyond the level of the bone's anterior articulatory facet. This expansion of the hyomandibula is probably correlated with the enlarged *levator arcus palatini* muscle. The entopterygoid and palatine bones are in contact.

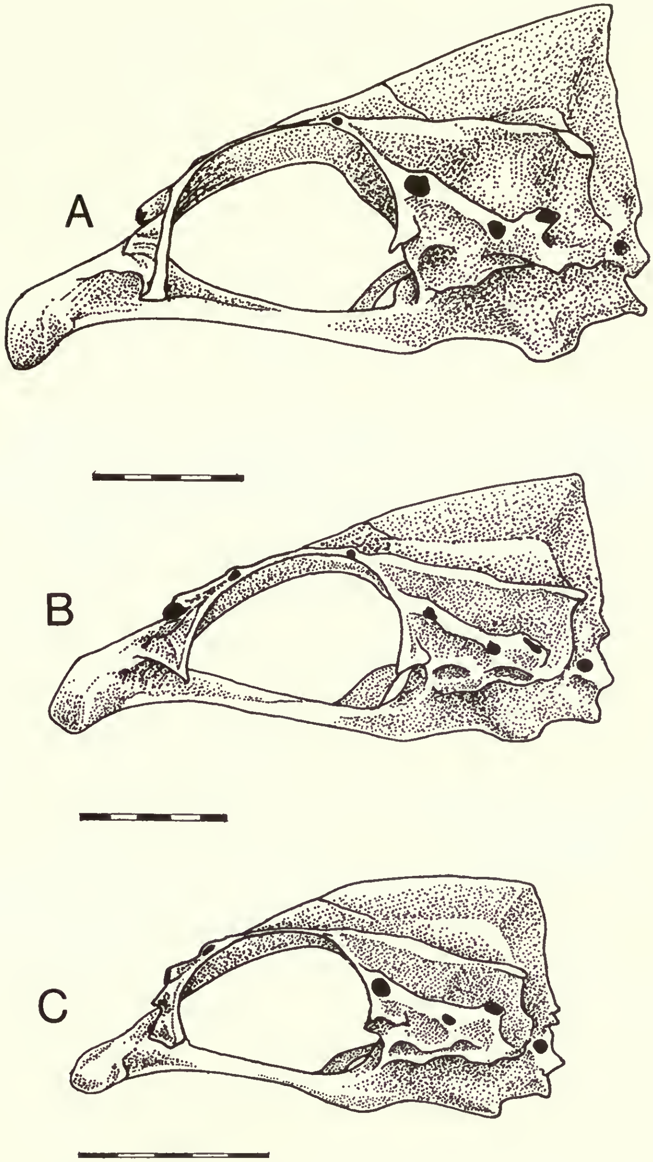

Fig. 10 Neurocranium, in left lateral view, of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Scale in mm.

Jaws. The dentigerous arms of the *premaxilla* are slightly inflated, the ascending processes are shorter than the dentigerous arms, and have but a slight posterior inclination (Fig. 8C).

The *lower jaw* (Fig. 11C), as compared with the generalized haplochromine condition, appears foreshortened in lateral view, with the coronoid arm of the dentary originating relatively far forward, and the region surrounding the dentary's division into horizontal and coronoid arms somewhat inflated. The outer tooth row extends posteriorly onto the anterior half, or slightly less, of the coronoid process.

The *dorsal gill-arch skeleton* was examined in 3 cleared specimens, double stained with alizarin-red and alcian-blue. Its most outstanding feature is the very greatly reduced cartilaginous extension from the anterior border of epibranchial II. In all African cichlids examined so far there is an expansive cartilaginous flange developed from this epibranchial, the flange extending forward and ventrally beyond the head of epibranchial I (see Stiassny, 1981: 294–296, and 1982: 430–432 for an account and figures of this feature in cichlids and related taxa).

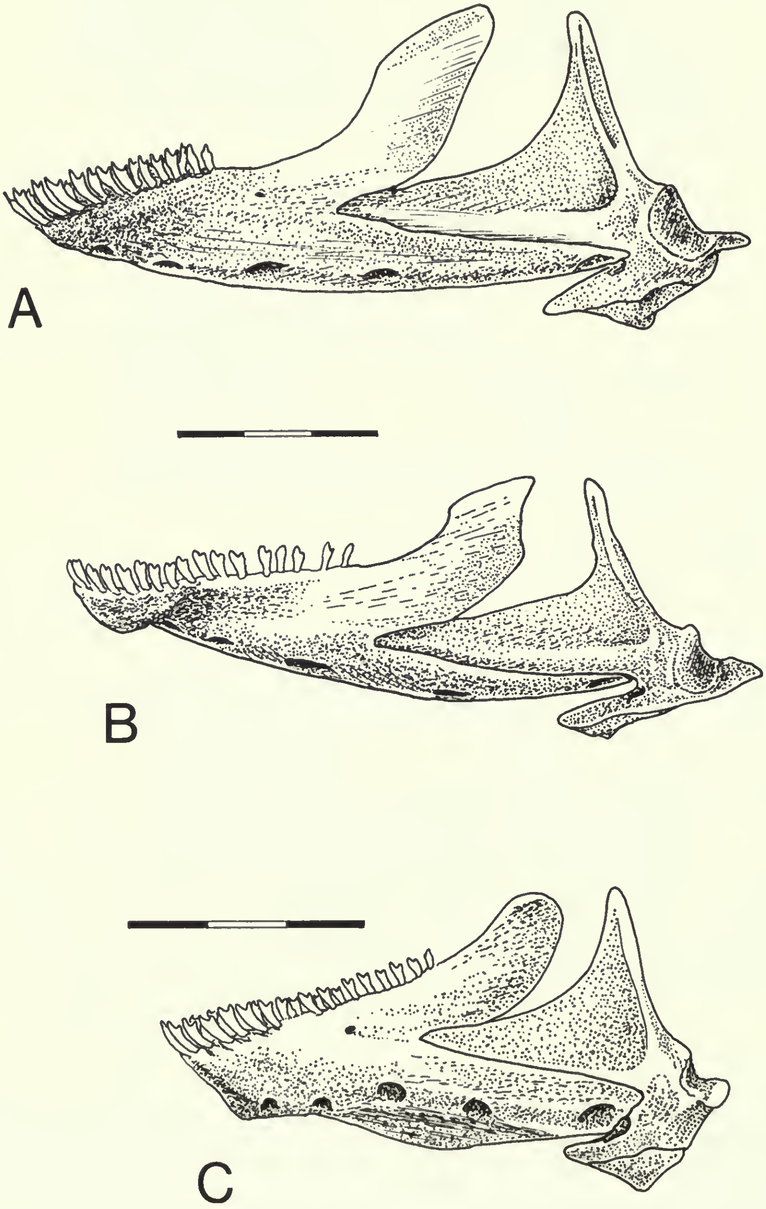

Fig. 11 Lower jaw, in left lateral view, of: A, *Thoracochromis buysi*; B, *Th. albolabris*; C, *Orthochromis machadoi*. Scale in mm.

In *O. machadoi* virtually no such extension is present, the margin of epibranchial II having merely a narrow strip of hyaline tissue (which is partly stained by the alcian blue). The strip is very slightly wider on the right than on the left side of the branchial skeleton, but on neither side is it broader or more extensive than the cartilaginous strip shown by Stiassny (1982: fig. 3) as occurring in the South American species *Cichla ocellaris*.

Regrettably, no double stained preparations are available for other *Orthochromis* species, and the feature cannot be checked on the dry skeletons available. Its significance, phylogenetically speaking, remains to be investigated.

Caudal fin skeleton. All eight specimens radiographed have hypurals 1 and 2, and 3 and 4 fused, as do the three alizarin transparencies examined. Such extensive and consistent fusion of hypural elements would seem to be a characteristic feature of the genus *Orthochromis* (Greenwood, 1979: 297).

Vertebrae. Excluding the fused PU_1 and U_1 centra, there are 28 (f2), 29 (f17) or 30 (f13) vertebrae, comprising 12 (f21) or 13 (f11) abdominal and 16 (f6), 17 (f20) or 18 (f6) caudal elements.

Breeding. As noted earlier, *O. machadoi* is apparently a female mouth-brooder. The smallest sexually active female recorded (apart from the brooding individual) is 46 mm SL, the smallest male, 52 mm. However, the preservation state for the majority of specimens examined precluded accurate determinations of sexual maturity or activity. Hence these figures can give only rough indications of the size at which sexual activity begins.

Coloration. Information is only available for formol fixed and alcohol preserved specimens. There are apparently no sexually correlated differences in preserved coloration; sexually active adults of both sexes are represented in the samples studied.

The ground coloration is a light brown (beige), usually shading to yellowish-brown ventrally. There are about twelve broad and dark 'bars' crossing the upper two-thirds to three-quarters of the body's lateral surface, the breadth of the 'bars' being about twice the width of the paler spaces between them. The 'bars' are not solid, but are formed from the dark outlines to the scales underlying the area which they occupy. The centres of these scales are lighter, so that the overall effect is to produce a diamond-mesh pattern of dark reticulations which, in places, are condensed to give the appearance of vertical bars. The centre of each 'bar' is darkest and is somewhat expanded anteroposteriorly, thus creating the appearance of an interrupted mid-lateral stripe; a similar but narrower and fainter stripe runs along the course of the upper lateral-line. At the base of the caudal fin there is a somewhat vertically elongate blotch.

The snout is crossed by two bands, the upper of which is the broader and becomes almost continuous with the darkly bordered scales on the nape and the posterior interorbital regions of the dorsum. A broad and intense lachrymal stripe runs from the orbit to the angle of the jaws, and is continued dorsally as a short blotch above the posterodorsal margin of the orbit. Post-orbitally there is a narrow horizontal bar continuous with the dark dorso-posterior margin of the operculum.

Dorsal, caudal and anal fins are a dusky hyaline, with the dark pigment most concentrated, almost into streaks, between the spinous rays of the dorsal fin. The lappets of that fin are clear. The anal is, apparently, without discrete maculae, and there are no indications of any ocellus-like spots. In males the pelvic fins are dark over their anterior third, and in females are hyaline with a faint dusting of small melanophores over the greater part of their surface.

Within the material examined there is considerable variation in the intensity of dark pigmentation, especially that contributing to the vertical 'bars'. However, within any one sample the intensity is generally constant. Whether this variation is attributable to differing preservation techniques, or is a reflection of populational differences or different environments, remains an open question.

DISTRIBUTION. The species is known only from the Cunene river; see also Poll (1967: 23 & 314), and p. 212 for detailed distribution records within the Cunene.

Study material and distribution records of *O. machadoi*

Registered material

BMNH;	P=collection no.	Locality
1972.9.27:90–91		Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:102–103	P612	Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).
1984.2.6:104–108	P1192	Cunene R., Calueque (17° 16′S, 14° 30′E)
1984.2.6:109	P672	Cunene R., 45 miles west of Ondurusu falls (17° 03′S, 13° 30′E).
1984.2.6:110–112	P696	Cunene R., above Epupa falls (17° 00′S, 13° 15′E).
1984.2.6:113	P713	Cunene R., above Epupa falls (17° 00′S, 13° 15′E).
1984.2.6:114–115	P716	Cunene R., above Epupa falls (17° 00′S, 13° 15°E).
1984.2.6:116–131	P1341	Cunene R., 82 km west of Ondurusu falls (16° 59′S, 13° 22′E).
1984.2.6:132–141	P1176	Cunene R., in the Chitapua falls (14° 23′S, 15° 18′E).
1984.2.6:142–145	P918	Cunene R., Folgares (14° 55′S, 15° 06′E).
1984.2.6:146	P882	Cunene R., Folgares (14° 55′S, 15° 06′E).

Unregistered material

Locality	Number of specimens	Collection no.
Cunene R., 10 miles west of Ruacana falls (17° 26′S, 14° 05′E).	2	P604
Cunene R., 5 km west of Ondurusu falls (17° 24′S, 13° 56′E).	10	P1392
Cunene R., Ondurusu falls (17° 24′S, 13° 56′E).	12	P1481
Cunene R., Calueque (17° 16′S, 14° 30′E).	2	P1192
Cunene R., 32 km west of Ondurusu falls (17° 15′S, 13° 23′E).	7	P1276
Cunene R., 32 km west of Ondurusu falls (17° 15′S, 13° 23′E).	9	P1278
Cunene R., 32 km west of Ondurusu falls (17° 15′S, 13° 23′E).	9	P1296
Cunene R., 32 km west of Ondurusu falls (17° 15′S, 13° 23′E).	17	P1299
Cunene R., Otjinungura (17° 12′S, 12° 20′E).	12	P1843
Cunene R., Otjinungura (17° 12′S, 12° 20′E).	1	P1324
Cunene R., 45 miles west of Ondurusu falls (17° 03′S, 13° 30′E).	12	P670
Cunene R., above Epupa falls (17° 00′S, 13° 15′E).	14	P705
Cunene R., above Epupa falls (17° 00′S, 13° 15′E).	8	P715
Cunene R., above Epupa falls (17° 00′S, 13° 15′E).	2	P697
Cunene R., above Epupa falls (17° 00′S, 13° 15′E).	1	P710
Cunene R., above Epupa falls (17° 00′S, 13° 15′E).	2	P1181
Cunene R., above Epupa falls, and 1 mile east.	4	P708
Cunene R., above Epupa falls, and 1 mile east.	1	P706
Cunene R., 82 km west of Ondurusu falls (16° 59′S, 13° 22′E).	2	P1290
Cunene R., 82 km west of Ondurusu falls (16° 59′S, 13° 22′E).	18	P1341
Cunene R., 82 km west of Ondurusu falls (16° 59′S, 13° 22′E).	10	P1361
Cunene R., 82 km west of Ondurusu falls (16° 59′S, 13° 22′E).	2	P1290
Cunene R., Folgares (14° 55′S, 15° 06′E).	10	P918
Cunene R., Folgares (14° 55′S, 15° 06′E).	13	P1345
Cunene R., Folgares (14° 55′S, 15° 06′E).	4	P882
Cunene R., Chitapua (14° 13′S, 15° 18′E).	2	P1116

DIAGNOSIS AND AFFINITIES. *Orthochromis machadoi* is easily distinguished from other Cunene haplochromines by several features. Amongst these may be noted its very small chest scales which are continuous with the small scales ventrally on the belly; the bilateral naked patches on the chest; the pelvic fins with the second and often the third branched ray longer than the first; the thickened skin covering the pelvic spine and first two or three branched rays; by the absence of discrete spots or ocelli on the anal fin of male fishes, and osteologically, by the low supraoccipital crest, the generally convex dorsum of the skull, and the greatly reduced cartilaginous projection from the anterior face of the second epibranchial bone.

In his original description of the species, Poll (1967: 314) commented on the similarity between the preserved colour pattern of *O. machadoi* and that of *Pseudocrenilabrus philander* (for which see p. 215). The new material of both species from the Cunene river, and elsewhere as well for *Ps. philander*, certainly confirms that similarity (but not the supposed phylogenetic affinity of the two species, as was suggested by Poll). However, the species are readily distinguished by their squamation patterns, especially that on the chest and belly, the sharp size differentiation between chest and ventrolateral flank scales in *O. machadoi*, the nature of the pelvic fins in that species, and in the different modal lateral-line scale counts for the two species (see p. 215 below). Furthermore, *Pseudocrenilabrus philander* is distinguished from *O. machadoi* and all other Cunene haplochromines in having 4 and not 5 lateral-line canal openings in the lachrymal (1st infraorbital) bone.

Despite the large amount of *O. machadoi* material now available, little more can be told about its possible intrageneric relationships (see Greenwood, 1979: 298). The species appears to be the least derived member of the genus, but even that supposition cannot be tested until more is known about its congeners.

PSEUDOCRENILABRUS Fowler, 1934

The diagnosis of this genus is based essentially on ethological features associated with the spawning habits of its constituent species. For details of these see Wickler (1963), in which paper he also erected the genus *Hemihaplochromis*, now treated as a synonym of *Pseudocrenilabrus* (see Trewavas, 1973: 33–36 for a full account of the taxon's nomenclatural history).

The sole morphological reflection of these ethological peculiarities is found in the absence of discrete spots, or of ocelli, on the anal fin of adult males. Instead, these markings are replaced functionally and morphologically by an orange or scarlet tip to that fin, a feature not readily discernible in preserved specimens. There are, however, two other features which, in the context of the Cunene haplochromines, serve to identify the genus, *viz*, the presence of only four openings in the first bone of the preorbital series (i.e. the lachrymal), and a tendency for there to be some, often several, pore-less scales in the lateral-line series. In those rare specimens with the entire lateral-line pored, only the four-pored lachrymal serves for instant diagnosis. The close superficial resemblance of the preserved coloration in Cunene *Orthochromis* and *Pseudocrenilabrus* species was commented on above; see also p. 215 below.

Currently, three species of *Pseudocrenilabrus* are recognised, *Ps. multicolor* (Schoeller, 1903), *Ps. ventralis* (Nichols, 1928) and *Ps. philander* (Weber, 1897). Their combined distributions extend, latitudinally, from the Nile to Natal, South Africa; no species occurs in north-west Africa.

The species-level taxonomy of *Pseudocrenilabrus* has not been revised for many years, and nothing is known about the phylogenetic relationships of the genus. Three subspecies of *Ps. philander* have been recognised (see Trewavas, 1936: 73, & 1973: 33–36), of which two, *Ps. philander dispersus* (Trewavas) 1936 and *Ps. p. luebberti* (Hilgendorf, 1902) occur within the Angolan region. The former subspecies is found in several rivers, including the

Cunene (Poll, 1967), but the latter is apparently restricted to sink-holes in the neighbourhood of Otavifontein, Namibia.

On the basis of one subspecifically diagnostic feature, the length of the premaxillary ascending process, the Cunene fishes I have examined would be referable to the subspecies *dispersus*, as was the Angolan material examined by Poll (1967). However, the Cunene material has a modal dorsal fin ray spine count of 15, and includes some specimens with 16 spines. On that character it should be referred to the subspecies *luebberti*.

Since these features appear to be the only trenchant ones on which the subspecies can be recognised (Trewavas, 1936: 7, and personal observations), I would argue that there is little to be gained from their formal recognition. A complete taxonomic overhaul of the genus is required, a revision that must take into account coloration and ethological features as well as anatomical ones, and must be based on numerous specimens from many localities. Until that revision is completed, I would also defer any decision on the validity of the third subspecies, *Ps. philander philander* (Weber) 1897, a taxon apparently restricted to Natal and Mozambique.

For these various reasons, and for others noted by Trewavas (1973: 33), the Angolan populations described here are recognised simply as *Ps. philander*.

Pseudocrenilabrus philander (Weber), 1897

SYNONYMY. See Trewavas (1936: 73)

DESCRIPTION. Based on 23 specimens from three localities (see p. 216). Since only ten fishes are undistorted the morphometric analysis is derived from those specimens alone, but meristic data were taken from the whole sample. Also, because of the small sample size, only ranges are given for morphometric characters. Where there are indications of populational differences in certain features, or where these fishes differ from those described by Poll (1967), comments are given between square brackets. Poll's material did include some specimens from the Cunene, but most came from the Cuango, Cuilo and Cassai river systems.

Depth of body 32·9–39·0% of standard length, length of head 34·2–38·8%.

Dorsal head profile sloping at an angle of 40°–45° to the horizontal, straight or gently curved from the nape to a point above the anterior orbital margin, then more strongly curved below that point.

Preorbital depth 12·9–18·2% of head length, the least interorbital width 19·2–25·8%. [Fishes from Jamba bridge, Cutato river, Cubango drainage, have a wider interorbital, 23·1–25·8, mean 21·6% of head, than those from the Cunene river at Calueque and from near Cafu; the range given by Poll for his entire sample is 18·1–24·6%.]

Snout 0·8–1·0 times as long as broad, its length 23·1–33·3% of head length.

Eye diameter 30·8–36·4% of head, cheek depth 16·7–25·0%.

Caudal peduncle 1·1–1·4 times longer than deep, its length 14·5–16·7% of standard length.

Mouth horizontal or almost so, the jaws equal anteriorly when the mouth is closed, the lips slightly thickened. The posterior tip of the maxilla reaches a vertical through the anterior orbital margin, or very nearly so.

Lower jaw 33·1–39·9% of head, 1·2–1·6 times longer than broad. The ascending processes of the premaxilla are 23·1–31·6% of head length.

Gill-rakers and pharynx. There are usually 8, rarely 9, short, stout and relatively compressed gill-rakers in the outer series on the lower part of the first gill-arch [Poll's count is 8–10, mode 8]. Microbranchiospines are present and obvious. The pharyngeal epithelium is not greatly thickened, nor is it deeply folded and papillose; the prepharyngeal pads are moderately developed.

Scales. There is a very gradual size transition between the scales on the chest and those on the ventrolateral aspects of the flanks and the ventral surfaces of the belly. The chest scales, although smaller than the belly scales, are not markedly smaller.

The lateral line-series has 27–30 (mode 28) scales. [In specimens from the Cutato river, 6–11 scales in the upper lateral-line, and 9–11 in the lower line, are without pores. Specimens from the two Cunene localities (see p. 216) have all the upper lateral-line scales pored, but from 2–7 scales in the lower line may lack openings. Poll makes no comments on this feature.] There are 4–5½ scales between the upper lateral-line and the dorsal fin origin, and 5 or, more frequently 6, between the pectoral and pelvic fin bases. The cheek has 3 rows of large scales which either cover the entire area or have a small naked embayment anteroventrally [Poll gives the range of cheek scale rows as 3–5].

There is never more than one large and one small scale between each of the last 8–14 upper lateral-line scales and the base of the dorsal fin [Poll makes no comments on this feature].

Fins. Dorsal with 14, 15 or 16 (mode 15) spinous and 8, 9 or 10 (modally 9 or 10) branched rays, anal with 3 spinous and 7–9 (mode 8) branched elements [The range given by Poll is: dorsal 13–15 spinous and 9–11 branched rays, modes 14 and 10 respectively; anal 3 spinous and 7–9, mode 8, branched rays.] No anal sheath scales were observed.

Caudal fin rounded, scaled on its basal quarter to third. Pectoral fin 22·5–25·4% of standard length, 61·5–69·2% of head length. Pelvics with the first branched ray slightly, but obviously longer than the second ray.

Teeth. In the outer row of both jaws the teeth are relatively stout and unequally bicuspid. The minor cusp lies at a slight angle to the broad-based major cusp; posteriorly in the upper jaw the last few teeth usually are unicuspid. There are 28–36 teeth in the outer row of the premaxilla [Poll gives a range of 35 to 63 teeth in this row, and indicates that the number is positively correlated with the fish's length; his sample included specimens longer than any recorded above].

Inner row teeth are tricuspid, with the middle cusp noticeably larger than the others, and are arranged in a single row in each jaw (except for one specimen which has a double row anteriorly and laterally in the lower jaw).

Lower pharyngeal bone and dentition. The shaft of the bone is relatively longer than that in any of the Cunene river or other *Thoracochromis* species; its length is contained about 1⅓ times in the length of the median tooth row (*cf* 1¾–2 times in *Thoracochromis* species). This feature contributes to the less attenuated appearance of the bone when it is compared with that of a *Thoracochromis* specimen.

The dentigerous surface is triangular and equilateral; the teeth are slender, compressed and cuspidate, those of the two median series being only a little coarser than the teeth in the lateral rows [Poll describes the teeth in his material as being 'conique', but I suspect this is an error].

Osteology. No skeletal material has been prepared. Vertebral counts (made from radiographs of the Cunene specimens) are: 25 (f1), 26 (f2), 27 (f3) and 28 (f2), comprising 12 (f5) or 13 (f3) abdominal and 13 (f1), 14 (f3) or 15 (f4) caudal elements.

It has proved impossible to produce radiographs suitable for observing the extent, if any, of hypural fusion and apposition.

Coloration. Only preserved colours are known for this material. Superficially, the coloration and colour pattern in *Ps. philander* closely resemble those of *Orthochromis machadoi* (see p. 211). They differ, however, in a number of details. The vertical bars on the flanks and caudal peduncle are solid; that is, the entire exposed surface of the scales underlying a bar is pigmented and not, as in *O. machadoi*, only the scale margins. Consequently, the diamond-mesh pattern so characteristic of *O. machadoi* is absent in *Ps. philander*. The bars in *Ps. philander* are less intense than those in *O. machadoi*, except in the region where each is expanded antero-posteriorly to form a faint and horizontal mid-lateral stripe; this restricted area of intensity results in *Ps. philander* having a more intense and discrete mid-lateral stripe. Similarly the upper longitudinal stripe is more distinct in *Ps. philander* than in *O. machadoi,* at least over the anterior half of the stripe's course. The species also differ in having the spot at the caudal fin base in *Ps. philander* less elongate and more distinct than that in *O. machadoi*.

The *dorsal fin* coloration in *Ps. philander* differs in having light spots on a dark background, the spots covering the membrane between the spines, and also in having light, slightly curved and narrow bands sloping obliquely across the dark membrane of the branched dorsal fin; the bands extend, with regular spacing, to the fin's posterior tip. The *caudal fin* also is banded, light on dark, but with the bands arranged vertically. The *anal, pelvic* and *pectoral* fins are hyaline, but the anal may be faintly banded by darker stripes running obliquely ventro-dorsad across most of its area. This anal banding is probably confined to males, or at least is more obvious in that sex; it seems to be the only sexually dimorphic feature apparent in the preserved coloration, apart from the faint, light spot at the posterior ventral tip of the anal which is sometimes visible in males.

Like *Orthochromis machadoi*, *Pseudocrenilabrus philander* has a prominent, but narrow, dark lachrymal, stripe; it lacks, however, the well-defined supraorbital continuation seen in *O. machadoi.* Unlike *O. machadoi* there are no transverse bands on the snout, which is dark grey in *Ps. philander.*

DISTRIBUTION. Widely distributed in southern Africa; for Angolan localities, see Poll (1967), and below.

DIAGNOSIS AND AFFINITIES. See discussion on pp. 213–214 above.

Study material and distribution records

Museum register number	Locality
BMNH; P = collection no.	
1984.2.6:64–74	Cunene R., pump station at Calueque (17° 16′S, 14° 30′E).
1984.2.6:75–76	Cunene R., near Cafu, Angola (16° 30′S, 15° 10′E).
1984.2.6:77–84	Cutato R., Jamba bridge, Angola (Cubango drainage)
1984.2.6:85–86	Okovango R., at Callindo, Angola

SERRANOCHROMIS Regan, 1920

The *Serranochromis* generic concept was redefined and expanded by Greenwood (1979: 299 *et seq*) to incorporate a number of species previously included in *Haplochromis.* These latter species, some of which had, at an earlier date (Regan, 1920) been placed in the genus *Sargochromis,* are now considered to form a subgenus of *Serranochromis.*

Reasons for uniting these various taxa phylogenetically are given by Greenwood (*op. cit.*), but an additional synapomorphy has been found as a result of comparative studies related to the Cunene representatives of both subgenera. This synapomorphy is the presence, in all species and most individuals, of two to four enlarged median teeth in the first row of the inner premaxillary series; these enlarged teeth are displaced a little anteriorly relative to the others in the row, and so come to lie between the first inner series and the outer tooth row (see figs 4, 9 & 13 in Trewavas, 1964). The majority of specimens I have examined show this displacement quite distinctly, although in a few it may appear only as an obvious irregularity in an otherwise uniformly curved tooth row.

SERRANOCHROMIS (SARGOCHROMIS) Regan, 1920

For a description and diagnosis of the subgenus, and a list of its constituent species, see Greenwood (1979: 303–305).

Considerable difficulty was experienced when attempting to identify the nine

Serranochromis (*Sargochromis*) specimens represented in the Penrith collection. Seven of these specimens were collected in the Cunene river, and two are from an affluent of the Cubango river. The latter apparently represent an undescribed species.

The most recent species-level revision of the taxa involved is that by Bell-Cross (1975), who recognised seven species. Only two of these, *S.* (*Sarg.*) *giardi* (Pellegrin) and *S.* (*Sarg.*) *coulteri* (Bell-Cross) are recorded from the Cunene system, with the latter taxon endemic to it.

Judging from Bell-Cross' descriptions, all seven *Serranochromis* (*Sargochromis*) species are identifiable, when alive, by their distinctive adult male coloration. For preserved material Bell-Cross provides a key employing what, apart from colour differences, seem to be the principal diagnostic features of the taxa. Using this key all the species, either individually or as small groups, should be determinable when, in various combinations, the form of the neurocranial pharyngeal apophysis, the morphology of the lower pharyngeal bone, the nature of its dentition and the shape of the head, are taken into account. Members of species groups, however, are usually separable only on the basis of their geographical distribution. For all species, the ranges of most meristic and morphometric characters show considerable overlap, although there is sometimes a distinction to be found in the mean or modal values for certain features. Such fine distinctions cannot, of course, be utilized when, as in the case of the present collection, only a few specimens are available for study.

From Bell-Cross' key there would seem to be little difficulty in distinguishing between the two species he recognised as occurring in the Cunene, namely *S.* (*Sarg.*) *giardi* and *S.* (*Sarg.*) *coulteri*. The former is characterized by its massive lower pharyngeal bone with an extensively molarized dentition, and its characteristically 'butterfly'-shaped pharyngeal apophysis (Bell-Cross, 1975: fig. 1 & pp 450–454; also p. 456). In sharp contrast, *S.* (*Sarg.*) *coulteri* has a weakly developed lower pharyngeal bone, the teeth of which are '. . . sharp and pointed' (Bell-Cross, 1975: 455; elsewhere [p. 429] the teeth in the median rows are described as '. . . slightly enlarged and not molariform'). The pharyngeal apophysis in this species does not depart from the modal *Haplochromis*-type (see Bell-Cross, 1975: fig. 1; also Greenwood, 1978: 303).

I would certainly confirm Bell-Cross' description of the *S.* (*Sarg.*) *giardi* pharyngeal bone and dentition, but must disagree with his account of those features in *S.* (*Sarg.*) *coulteri*. Using the material (both whole specimens and skeletal preparations) on which Bell-Cross (1975: 426–431) based his description of *S.* (*Sarg.*) *coulteri* I find that, apart from the smallest fish in the size range it covers (105–214 mm SL), at least the two median tooth rows, and often most teeth in the next two lateral rows, are composed of enlarged teeth with flat, molar-like crowns and cylindrical necks (Figs 12–15). Morphologically, these teeth are quite distinct from the compressed, shouldered and thus virtually bicuspid teeth occurring in the lateral and posterior dentigerous fields of the bone. Only in the smallest specimen (105 mm SL, BMNH 1975.6.19: 1–13; DA68) do the median teeth retain slight indications of a minor cusp, and a discrete posterior cusp (Fig. 13). In other words, apart from their manifestly coarser appearance, the median teeth in this specimen are like those situated posteriorly and medio-laterally on the bone. This specimen alone, would accord with the description Bell-Cross gives for the pharyngeal dentition in *S.* (*Sarg.*) *coulteri*.

Thus, I cannot agree with Bell-Cross' description, in his key, of the pharyngeal teeth in *S.* (*Sarg.*) *coulteri* as being 'sharp and pointed' (even the lateral teeth are bicuspid), and would consider his description in the text ('teeth slightly enlarged') to be an understatement, at least with respect to fishes more than 105 mm SL. Likewise, I would argue against his statement (*loc. cit.*) that the crowns are 'not molariform'; they are molariform in large specimens, and could be described as 'submolariform' in all others except the smallest fish.

With that correction made, the situation regarding the specific identification of preserved *Serranochromis* (*Sargochromis*) material is rendered more difficult. The lower pharyngeal dentition in *S.* (*Sarg.*) *coulteri* is, in fact, like that in many specimens of supposed *S.* (*Sarg.*) *codringtoni* and *S.* (*Sarg.*) *mellandi*, and there are no trenchant meristic or morphometric features which can be used to separate elements of the trio.

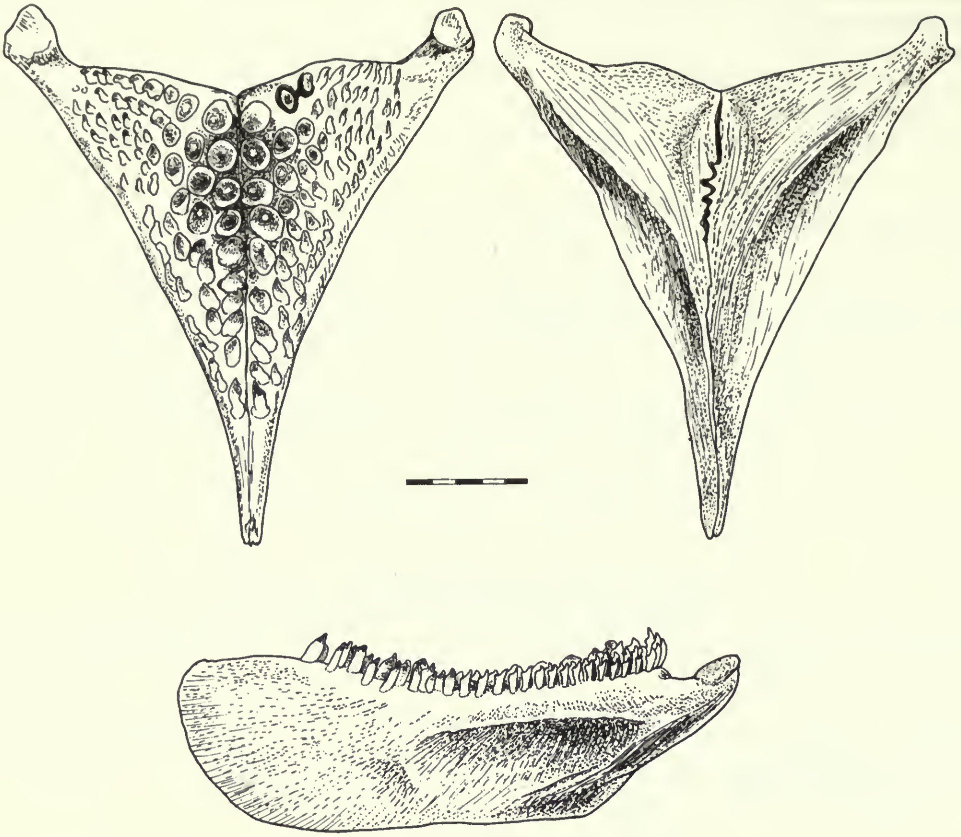

Fig. 12 *Serranochromis* (*Sargochromis*) *coulteri*. Lower pharyngeal bone of the holotype, a specimen 216 mm SL from the Cunene river system. Scale in mm.

An examination of several specimens identified either as *codringtoni* or *mellandi* shows that there is a wide range in the degree to which the lower pharyngeal dentition is molarized, and a correlated variation in the degree to which the bone is enlarged. In some specimens both bone thickening and tooth molarization exceed that found in *S.* (*Sarg.*) *coulteri*, but in many others there is complete overlap with the conditions found in that species.

In one respect, overall tooth shape, the enlarged teeth in *S.* (*Sarg.*) *coulteri* do seem to differ from those in the other two species. Whereas the teeth in *S.* (*Sarg.*) *mellandi* and *S.* (*Sarg.*) *codringtoni* are short and broad, those in *S.* (*Sarg.*) *coulteri* are relatively taller and more slender, features particularly obvious in smaller specimens. Also, in *S.* (*Sarg.*) *coulteri* the posterior horns of the pharyngeal bone appear to be rather more slender than those in the other two species, even when the dentition and bone itself are at comparable levels of hypertrophy.

On the basis of overall pharyngeal tooth morphology, I would therefore refer, at least tentatively, four Cunene river specimens (76·5, 98·0, 130·0 and 132·0 mm SL respectively to *S.* (*Sarg.*) *coulteri*; for detailed distribution records see p. 230.

These presumed *S.* (*Sarg.*) *coulteri* differ in some respects from the specimens described by Bell-Cross (1975), but it should be recalled that two are smaller than any of the specimens he examined. In two of the new specimens (76·5 and 98·0 mm SL) eye diameter is larger (30·3% of head length), and the snout is shorter (32·1 and 33·0% head in the specimens

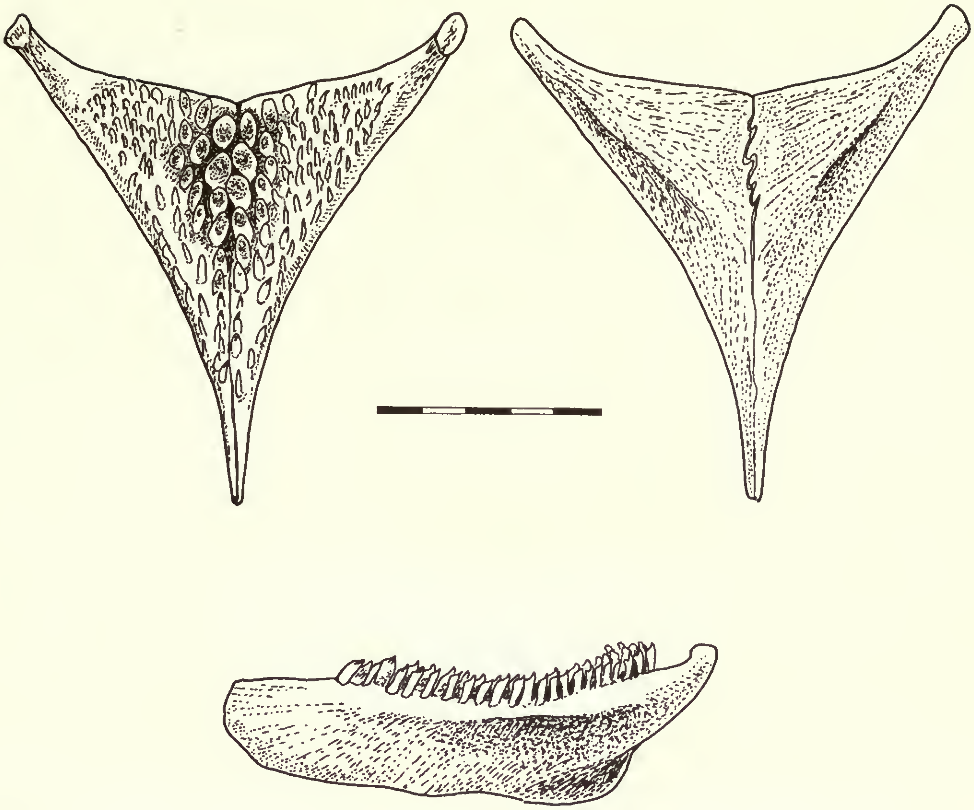

Fig. 13 *Serranochromis* (*Sargochromis*) *coulteri.* Lower pharyngeal bone from a specimen 105 mm SL (1975.6.19: 1–3; DA68, *ex* Cunene river system). Scale in mm.

respectively); the four specimens have slightly shorter lower jaws (33·9–37·0% head *cf* 37·4–42·6% in the Bell-Cross material). All other morphometric features lie within the ranges given by Bell-Cross.

In some meristic characters the new material also lies outside the ranges given by Bell-Cross (1975: table in appendix (iii)). Three of the four specimens (including the two smallest) have 12 or 13 gill-rakers on the first arch (9–11, mode 10, according to Bell-Cross), and all have higher lateral-line scale counts (33 or 34, *cf* 30–31, mode 31).

Clearly some of these discrepancies might be attributable to personal differences in the way counts and measurements were made, and others could be attributed to the smaller size of two specimens I examined. Parenthetically it should be mentioned that Bell-Cross' (1975: 429) statement that the first branched pelvic ray in *S.* (*Sarg.*) *coulteri* reaches the origin of the anal fin, does not hold for specimens other than the type; probably the length of this ray is correlated with an individual's sex and, in the case of adult males, with the level of sexual activity. Also, it should be noted that the photograph of the type specimen reproduced in Bell-Cross (1975: plate 4) was taken before the fish was set and preserved. The distended mouth shown in the picture distorts the dorsal head profile which, in the preserved specimen, is like that in most other *Serranochromis* (*Sargochromis*) species; see, for example plates 5, 6 and 8 in Bell-Cross (1975).

Of the remaining new *Serranochromis* (*Sargochromis*) specimens, one large fish (270 mm

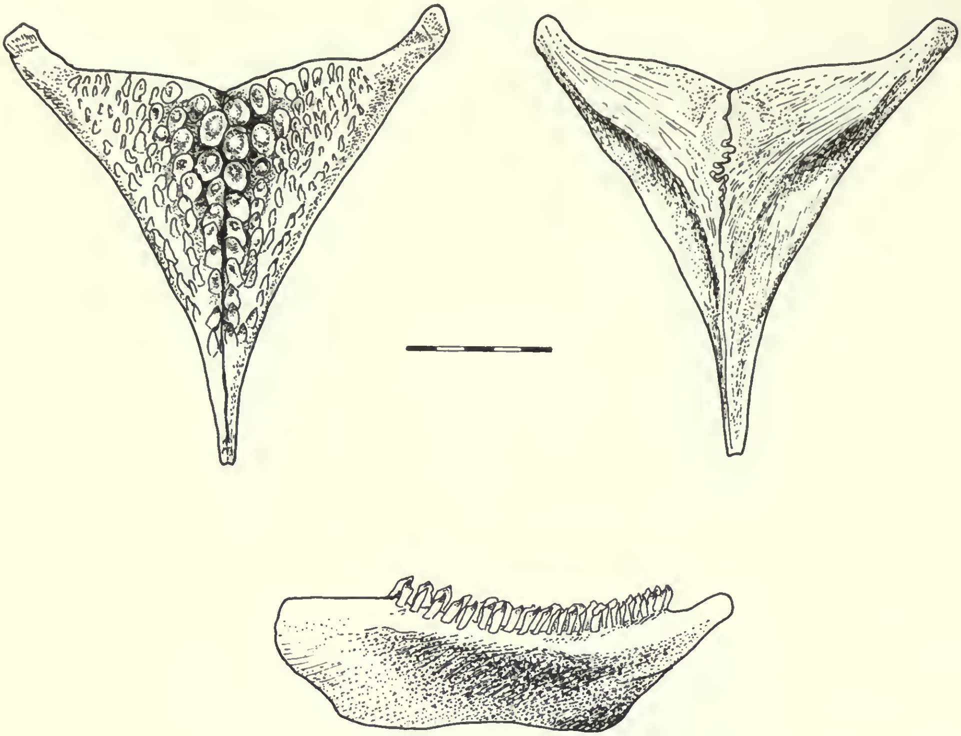

Fig. 14 *Serranochromis* (*Sargochromis*) *coulteri*. Lower pharyngeal bone from a specimen 139 mm SL (1975.6.19: 1–3; DA59, *ex* Cunene river system). Scale in mm.

SL, BMNH 1984.2.8: 1) should, on the basis of its extremely hypertrophied lower pharyngeal bone and the extreme molarization of its teeth (Fig. 16), be identified as *S.* (*Sarg.*) *giardi* (see Bell-Cross, 1975: 451–454). In its general appearance too, particularly the almost rounded head profile, this specimen resembles *S.* (*Sarg.*) *giardi* from localities outside the Cunene system. However, it differs from those fishes in certain morphometric features, as it does from the few Cunene specimens currently identified as *S.* (*Sarg.*) *giardi*. These other Cunene specimens comprise three small fishes (the largest 86·0 mm SL) from Ponang Kuma, Mossamedes (probably Donguena, 17° 03´S, 14° 40´E, according to Dr Michael Penrith, *in litt*). They were previously identified by Boulenger (1915: 408) and by Regan (1922: 263) as *Sargochromis angolensis* (Steindachner), but were reidentified as *Haplochromis giardi* by Bell-Cross (1975).

The new 270 mm long specimen comes from below the Ruacana falls (17° 24´S 14° 13´E) is larger than any of the *giardi* material examined by Bell-Cross, all of which, save that from Ponang Kuma, came from the Okovango, Zambezi or Kafue river systems. It also differs from those specimens in having a greater preorbital depth (26·1% of head *cf* 19·4–22·3, mean 21·2%), and a longer lower pharyngeal bone (43·2% of head, *cf* 37·6–41·8%). The pharyngeal apophysis, however, has the specifically characteristic 'butterfly' shape described by Bell-Cross (1975: 453 and 411; fig. 1), and is of the extreme 'butterfly' type (as might be expected from the great hypertrophy of the pharyngeal mill) which otherwise occurs in fishes from the Zambezi (see Bell-Cross, 1975; fig. 1).

If it be assumed that the deeper preorbital bone (lachrymal), and the longer pharyngeal

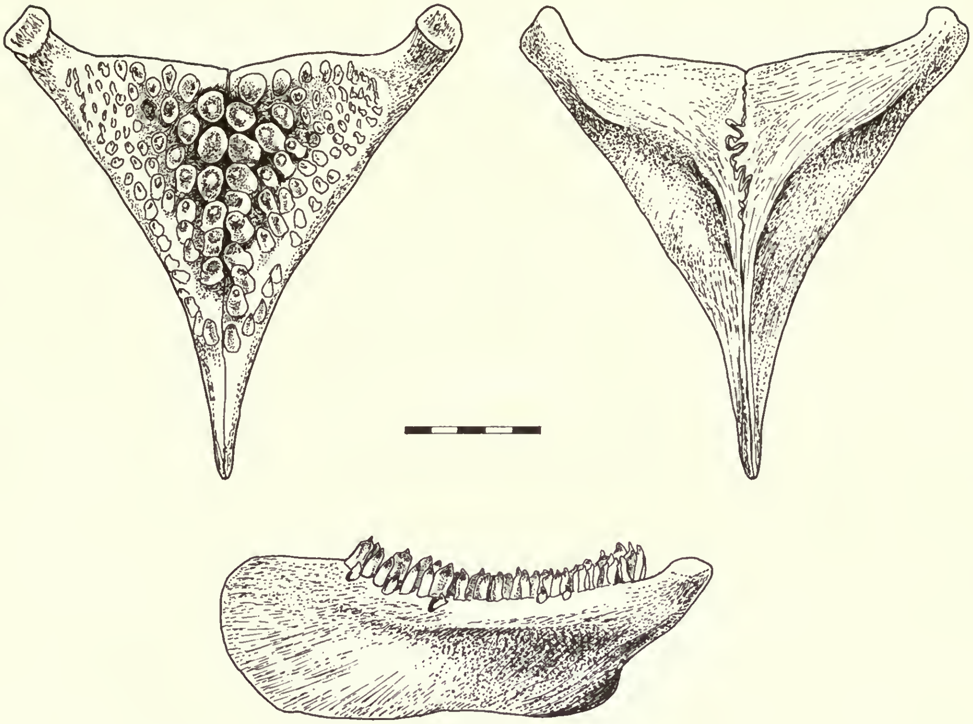

Fig. 15 *Serranochromis* (*Sargochromis*) *coulteri*. Lower pharyngeal bone from a specimen 183 mm SL (1975.6.19: 1–13; DA54, *ex* Cunene river system). Scale in mm.

bone in the new Cunene fish are both correlates of that specimen's large size (or are simply examples of individual variability), this fish could be identified as *S.* (*Sarg.*) *giardi*. However, certain other Cunene specimens throw some doubt on that conclusion.

One of these specimens is another large fish, 190 mm SL (BMNH 1984.2.6: 149), and comes from a locality 45 miles west of Ondurusu Falls (17° 03´S, 13° 30´E). It too has an hypertrophied lower pharyngeal bone with an extensively molarized dentition, and its pharyngeal apophysis approaches the extreme 'butterfly' type, being intermediate between the Kafue and Upper Zambezi forms illustrated by Bell-Cross (1975, fig. 1). The lower pharyngeal bone, however, proves to be less massive, and its dentition less molarized than in *S.* (*Sarg.*) *giardi* of a comparable size. It is more massive and further molarized than in a 260 mm specimen of *S.* (*Sarg.*) *codringtoni*, but only slightly more massive and molarized than in a 194 mm specimen of the same species. Similar results are obtained when the Cunene specimen is compared with examples of *S.* (*Sarg.*) *mellandi.*

The 190 mm Cunene specimen, like the 270 mm fish discussed earlier, differs from individuals in other populations of *S.* (*Sarg.*) *giardi* in having a deeper preorbital (27·1% of head, *cf* 18·0–22·0, mean 19·9% in *S.* (*Sarg.*) *giardi*) but unlike the larger Cunene fish it also differs in having a somewhat shorter lower jaw (34·2% of head, *cf* 36·0–42·6, mean 39·6%).

Although the lower pharyngeal bone and dentition in the 190 mm Cunene specimen are comparable, except for the bone's greater length (which does lie within the *giardi* range), with those in some specimens of *codringtoni* and *mellandi*, the short lower jaw would seem to exclude the specimen from either of these taxa, as well as from *giardi.* Its preorbital depth,

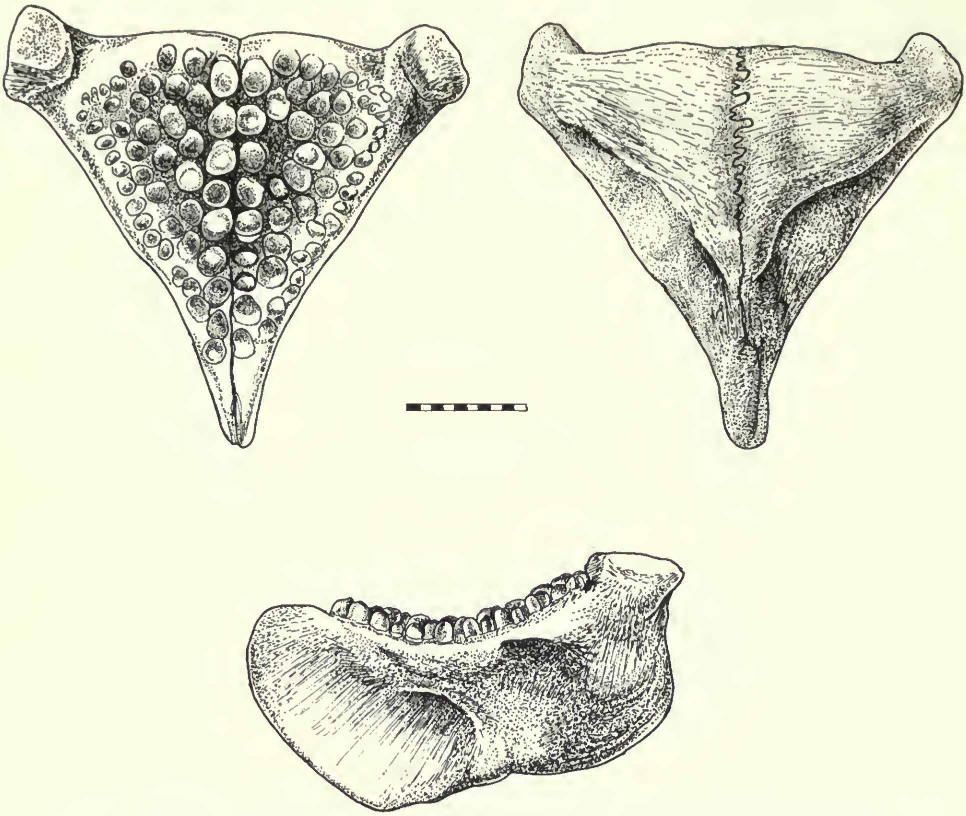

Fig. 16 Lower pharyngeal bone from a *giardi*-like member of the *Serranochromis* (*Sargochromis*) *giardi-codringtoni* species complex, 270 mm SL, *ex* Cunene river (1984.2.8: 1). Scale in mm.

excessive for *giardi* is, however, only a little greater than the maximum recorded for either *mellandi* or *codringtoni.*

The larger (270 mm) specimen, it will be recalled, has a more massive pharyngeal mill than is found in specimens of either *mellandi* or *codringtoni*, but that 'gap' is bridged by the bone and its dentition in the 190 mm fish. Lower jaw length in the larger fish, however, lies within the ranges for *giardi*, *codringtoni* and *mellandi*, and its preorbital depth lies within the ranges for *codringtoni* and *mellandi*, but outside that for *giardi.* In other words, on morphometric characters and in the nature of the pharyngeal mill, the two *giardi*-like fishes from the Cunene seem to show, either in the themselves or by providing bridging features, characters of three *Serranochromis* (*Sargochromis*) species, only one of which (*giardi*) is thought to occur in that river.

This situation is by no means clarified when two further specimens, 122 and 190 mm SL, from the Hamburg Museum collections, are taken into account. These fishes (ZMH 1722, collected in the Cunene at Capelongo) have greatly hypertrophied lower pharyngeal bones with extremely molarized dentitions. On those criteria the specimens fall within the range of variation encountered within *S.* (*Sarg.*) *giardi*, *mellandi* and *codringtoni* (Fig. 17) but are perhaps nearest *giardi.* The length of the bone (33·5% of head length) for the larger of the two Hamburg specimens, however, is below that for *giardi* of a comparable length, is near but slightly shorter than that for *codringtoni*, and is well within the range for *mellandi.* The

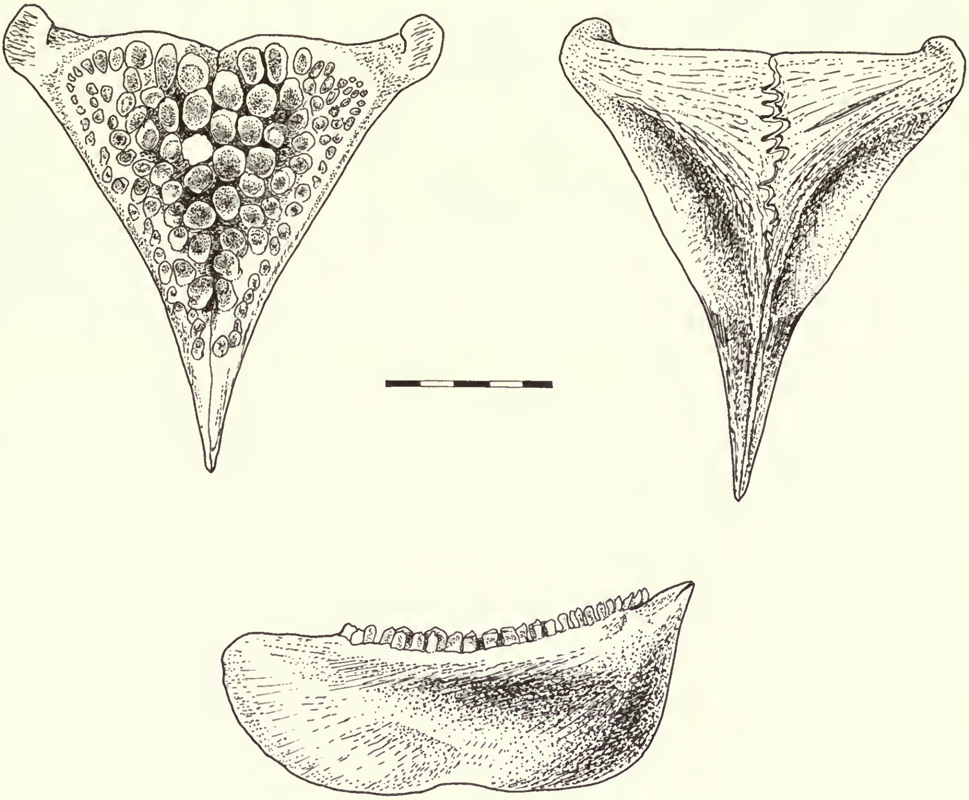

Fig. 17 *Serranochromis* (*Sargochromis*) *codringtoni*. Lower pharyngeal bone from a specimen 183 mm SL (1975.6.19: 1–3; *ex* Kafue river). Scale in mm.

length of the bone in the smaller fish, 33·3% of the head, falls within the recorded ranges for comparable sized *mellandi* and *codringtoni*, but is below that for *giardi* of the same length.

Preorbital depth in the larger Hamburg specimen (25·0% of head) is somewhat greater than that recorded for *giardi*, but closely approaches that for *codringtoni* and *mellandi*; in the smaller fish, the preorbital depth (21·0% of head) lies within the range for comparable sized *giardi*, *codringtoni* and *mellandi*.

Lower jaw length in the larger Hamburg fish (35·8% of head) is slightly below that of *giardi*, and also below that of *codringtoni*, but is much shorter than in *mellandi*; the smaller specimen, however, has a jaw length (38·0% of head) within the ranges for all three species.

Taken in concert, the features in the two Hamburg specimens, and those of the two Cunene fishes, certainly seem to break down the principal morpho-anatomical differences between *Serranochromis* (*Sargochromis*) *giardi* and *S.* (*Sarg.*) *codringtoni*, and, indeed, those between these species and *S.* (*Sarg.*) *mellandi*.

This conclusion casts doubts on any possibility of identifying the new Cunene specimens with enlarged pharyngeal mills. The small specimens from Ponang Kuma (see above, p. 220) can be identified as *giardi* on the basis of various 'key' characters. But, in the absence of specimens at sizes intermediate between them and the larger fishes discussed above, even that identification is uncertain.

Clearly the situation is confused, and is unlikely to be clarified without studying a lot more material, supported by data on breeding coloration, from all areas in which the species *giardi*, *mellandi* and *codringtoni* have been recorded. Until that revision is effected, I would prefer to recognize the Cunene specimens with hypertrophied pharyngeal mills only as members of a *Serranochromis* (*Sargochromis*) *giardi-codringtoni* species-complex, that complex to include *S.* (*Sarg.*) *mellandi.* Certainly it would be unrealistic to refer the Cunene specimens to any one species in that complex; to describe them as a new species would confuse the issues involved.

I suspect that specimens from Lake Calundo, Angola, described by Poll (1967) and identified by him as *Haplochromis mellandi,* are also members of the '*giardi-codringtoni*' complex. Poll's figure (1967: fig. 50, p. 310), and his remarks about the deep preorbital in these fishes, reinforce my suspicions. Bell-Cross (1975: 436) thought that Poll's specimens should be referred to *S.* (*Sarg.*) *codringtoni*, a taxon which I would include in the complex under discussion.

At this point it is appropriate to mention certain type specimens of Boulenger's (1913) species *Tilapia steindachneri* (see p. 189). The specimens in question (BMNH 1907.6.29: 176–9; from the Donguena swamps) were later referred to *Sargochromis mellandi* [now *Serranochromis* (*Sargochromis*) *mellandi*] by Regan (1922: 263), a decision with which I would concur, allowances being made for the species-level problems discussed above. All are small fishes (52·0–64·0 mm SL). One, the largest, was illustrated by Boulenger (1915: 210; fig. 134) and designated 'Type' in the caption to the figure accompanying this redescription of the species. That action I treat as the subsequent designation of a type specimen since none was chosen when the species was first described (Boulenger, 1913).

The figured specimen and three others from Donguena swamp are easily distinguished from the remaining syntypes of *Tilapia steindachneri*, collected in the Que river, a tributary of the Cunene. The Que fishes are now referred to *Thoracochromis buysi* (Penrith); see p. 190.

The type and three syntypes of *Tilapia steindachneri* from Donguena swamp have enlarged lower pharyngeal bones, with most teeth in the two median rows enlarged and molariform or submolariform, and thus resemble those in *Serranochromis* (*Sargochromis*) *codringtoni* and *S.* (*Sarg.*) *mellandi.* Considering the small size of these fishes, and the degree to which their lower pharyngeal bones are enlarged, it seems likely that, as adults, they would have relatively massive to massive pharyngeal bones, and a highly molarized dentition. Unfortunately there is no way in which the four specimens can be given a positive specific identification, especially in the light of what is now known about the possible complex of *Serranochromis* (*Sargochromis*) species in Angola (see p. 217). Under the circumstances it would seem inadvisable to consider the synonymy of *Tilapia steindachneri* (in part) with *Serranochromis* (*Sargochromis*) *mellandi* as well established. The question should be left open until the Angolan '*giardi-codringtoni*' complex is resolved. From that complex could well emerge a taxon which would take the name '*steindachneri*'.

Finally, attention must be given to another *Serranochromis* (*Sargochromis*) specimen amongst the new material from the Cunene river. This fish, 126 mm SL (BMNH 1984.2.6: 154) is apparently referable to the species *S.* (*Sarg.*) *greenwoodi* (Bell-Cross), a taxon not previously recorded from Angola; all other records are from the Upper Zambezi, Kafue and Okavango river systems. Apart from the new species to be described below, *S.* (*Sarg.*) *greenwoodi* is unique amongst the species of this subgenus in having, at least in most populations, a fine lower pharyngeal bone with no noticeably enlarged or molarized teeth (see Bell-Cross, 1975: 425).

The Cunene specimen, from Matala Dam, Luceque (14° 36´S, 15° 18´E) is an adult male. It has a relatively slender lower pharyngeal bone (length 27·6% of head length) whose dentition is composed mainly of fine bicuspid teeth; a few teeth in the posterior part of the two median rows are somewhat enlarged, but, like the others, are distinctly bicuspid. In all morphometric features, including a deep preorbital bone (27·6% of head), long snout (42·5% of head), long lower jaw (42·5% of head), and long ascending premaxillary processes (34·5% of head), the specimen falls within the range for *S.* (*Sarg.*) *greenwoodi* from other localities.

Its dental and meristic characters are also within the range of that species, and include the high gill-raker count of 14. Despite our apparently identical methods for counting the lateral-line scale series (Bell-Cross, 1975: 410), I make the number of scales in *S.* (*Sarg.*) *greenwoodi* 33–36, and not, *pace* Bell-Cross, 29–31. The Cunene fish has a count of 33.

Although this fish resembles *S.* (*Sarg.*) *greenwoodi* in all features ascertainable from a single, preserved specimen, its precise status will be uncertain until more material is available, and data are obtained on the live colours of breeding males.

The two remaining *Serranochromis* (*Sargochromis*) specimens in the Penrith collection were obtained from the Cubango river drainage basin. They are conspecific, but do not seem referable to any of the species or populations so far described.

I am loath to create a new taxon on only two specimens, especially since the taxonomy of the subgenus *Sargochromis* is in such an uncertain state. However, the specimens are very distinctive and thus would seem to justify their recognition as members of a new species.

***Serranochromis* (*Sargochromis*) *gracilis* sp. nov.**

(Fig. 18)

HOLOTYPE. An adult female, 116·5 mm standard length, from the Cutato river at Jamba bridge (Cubango drainage), Angola; BMNH 1984.2.6: 147. Paratype: an adult female 118·0 mm SL, from the same locality; BMNH 1984.2.6: 148.

The trivial name, from the Latin, meaning slender or simple, refers to the body proportions of the type specimens, and to the relatively unspecialized nature of the pharyngeal dentition.

DESCRIPTION. Based on the two types specimens only.

Depth of body 33·1 and 34·3% of standard length, length of head 36·9 and 37·3%.

Dorsal head profile gently curved and sloping at an angle of *ca* 30°–35° to the horizontal.

Preorbital depth 18·6 and 19·3 of head length, least interorbital width 18·2 and 18·6%. Snout 1·1 and 1·2 times longer than broad, its length 31·8 and 33·7% of head. Eye diameter 25·0 and 25·6% of head, depth of cheek 22·7 and 23·3%.

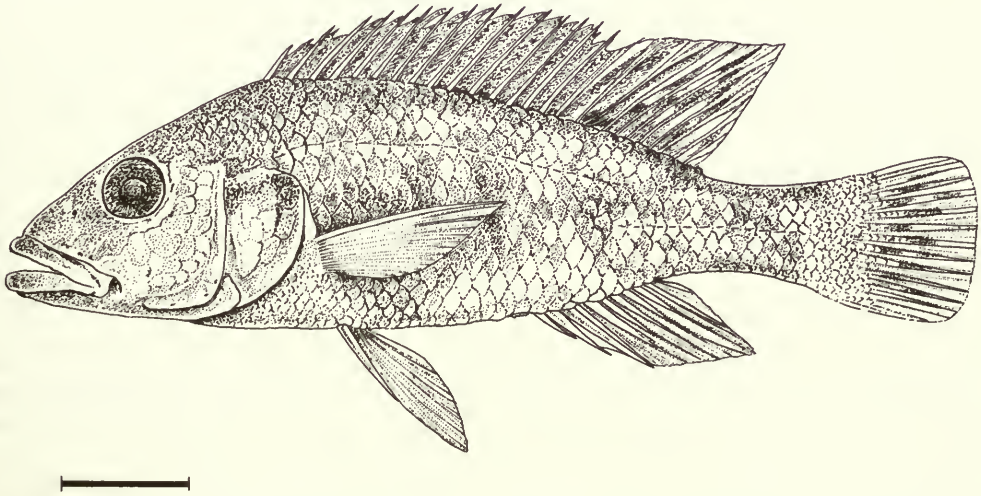

Fig. 18 *Serranochromis* (*Sargochromis*) *gracilis*. Holotype. Drawn by G. J. Howes. Scale = 18 mm.

Caudal peduncle 1·4 and 1·5 times longer than deep, its length 15·4 and 16·1% of standard length.

Mouth very slightly oblique, sloping at an angle of *ca* 15° to the horizontal; lips slightly thickened, jaws equal anteriorly when the mouth is closed. Posterior tip of the maxilla reaching a vertical through the anterior orbital margin; premaxilla not beaked anteriorly, its ascending processes breaking, slightly, the dorsal outline of the head, their length 31·8 and 32·5% of the head.

Gill-rakers. Ten in the outer row on the lower part of the first gill arch, the lowest one or two rakers greatly reduced, the following 5 or 6 either stout and short (holotype) or relatively slender, the uppermost 3 rakers either flattened, with the crown produced into 2 or 3 cusps, or flattened and anvil-shaped (holotype). Microbranchiospines are present.

Scales on the anterior part of the body below the lateral-line are weakly ctenoid, but are cycloid above that level. Scales on the posterior part of the body are cycloid. When ctenoid, the scales have the cteni distributed over most of the exposed parts. The chest scales are not noticeably small, and have a gradual size gradient with those on the belly and ventrolateral aspects of the flanks.

Lateral-line with 34 scales, cheek with 4 rows of large scales which cover the area except for a small naked embayment anteroventrally. There are 5 scales between the dorsal fin origin and the lateral-line, 7 between the pelvic and pectoral fin bases. Only the last (holotype), or the last two, pored scales of the upper lateral-line are separated from the dorsal fin base by one large and one small scale, the others being separated from the fin by at least 2 large scales of almost equal size.

Fins. Dorsal with 15 spinous and 13 branched rays, anal with 3 spines and 10 branched elements. No anal sheath scales are present in either specimen. Pectoral fin 22·3 and 22·9% of standard length. Caudal subtruncate, scaled over its basal two-thirds or three-quarters. First branched pelvic ray not reaching the vent.

Teeth. The *outer row* in both jaws is composed of relatively slender and compressed teeth. In most the crown has a sharp, fine point and a low, laterally placed shoulder; other teeth in the row are more distinctly bicuspid, the shoulder being replaced by a discrete minor cusp. Posteriorly, there is a short edentulous region on the premaxilla. About 50 and 54 teeth are present in the premaxillary outer row.

The *inner teeth* are mostly tricuspid or weakly bicuspid, but a few unicuspids occur anteriorly; the teeth are arranged in a single row in both jaws, that of the upper jaw extending posteriorly beyond the anterolateral section of the bone's dentigerous surface. Medially in the upper jaw there are two enlarged teeth situated between the inner and outer tooth rows.

Lower pharyngeal bone and dentition (Fig. 19): The bone is not enlarged, its teeth are distinctly cuspidate, with the minor cusp present as either a well-demarcated shoulder or a discrete cusp. Teeth in the two median rows are manifestly coarser and larger than those situated laterally and postero-laterally. The dentigerous area is a little longer than broad, giving it a more nearly isoscelene than equilateral outline. The length of the bone, measured in one specimen, is 28·0% of the head length.

Osteology. No skeleton is available but both specimens were radiographed. Excluding the fused PU_1 and U_1 centra, there are 31 vertebrae, comprising 15 abdominal and 16 caudal elements. In the one specimen dissected the neurocranial pharyngeal apophysis is of the typical *Haplochromis*-type, although the basioccipital contributions to the facet are not extensive.

Judging from the radiographs, the neurocranium has a relatively protracted ethmovomerine region. Comparison with figures in plates 1 & 2 of Bell-Cross (1975) suggests that of the skull of *S.* (*Sarg.*) *gracilis* is nearest that of *S.* (*Sarg.*) *greenwoodi*, a resemblance confirmed by comparisons with actual skulls.

Coloration. Live colours are unknown. The two formol preserved and alcohol fixed specimens have a pale beige ground coloration which darkens dorsally and lightens ventrally; the dorsal surface of the head and snout is greyish. Traces of up to eight vertical bars cross the flank and caudal peduncle, and are most obvious over the midlateral surfaces of the flanks;

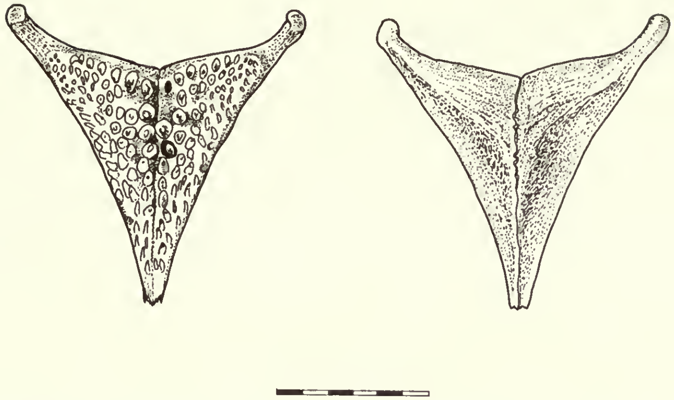

Fig. 19 *Serranochromis* (*Sargochromis*) *gracilis.* Lower pharyngeal bone. Scale in mm.

dorsally the bars merge with the darker ground colour, ventrally they terminate along a horizontal line drawn posteriorly from the base of the pectoral fin. A pronounced opercular spot is present, but no other cephalic markings are apparent.

The entire *dorsal fin* is densely flecked with brownish to reddish streaks and elongate spots, the markings becoming more discrete on the soft parts of the fin; the lappets to the spinous dorsal have a similar dark pigmentation. The *caudal fin*, to about its distal quarter, is darkly spotted with elongate ovoid maculae; the distal quarter of the fin is hyaline, with traces of a dark but narrow marginal band, more obvious in one specimen than the other. The *pectoral*, *pelvic* and *anal fins* are hyaline; the soft part of the anal is lightly maculate, the spots fairly regularly arranged in two rows.

Breeding. Both specimens are adult females at an advanced stage of oogenesis; the left and right ovaries are equally developed.

Distribution. Known only from the Cutato river, Angola.

Diagnosis. The relatively slender, unthickened lower pharyngeal bone of *S.* (*Sarg.*) *gracilis*, with its distinctly bicuspid teeth, sets the species apart from all members of the subgenus except *S.* (*Sarg.*) *greenwoodi* and some individuals of *S.* (*Sarg.*) *coulteri* (see p. 217).

The compressed outer row teeth in the jaws, the persistence in that row of bi- and weakly bicuspid teeth in specimens over 100 mm SL, and the persistence in such individuals of numerous tricuspid teeth in the inner tooth rows, distinguish *S.* (*Sarg.*) *gracilis* from both *S.* (*Sarg.*) *greenwoodi* and *S.* (*Sarg.*) *coulteri*, and from the other species as well. The gently sloping dorsal head profile, and the shallow body of *S.* (*Sarg.*) *gracilis* are further diagnostic features.

More specifically, *S.* (*Sarg.*) *gracilis* is distinguished from the two species with fine pharyngeal bones and dentition as follows:

From *S.* (*Sarg.*) *greenwoodi* by its shorter pectoral fins (22·3–22·9% SL *cf* 25·6–29·2, mean 27·7%), shorter snout (31·8–33·7% head, *cf* 37·4–40·7, M = 39·3%), shallower preorbital bone (18·6–19·3% head, *cf* 25·3–27·3, M = 26·3%), narrower interorbital width (18·2–18·6% head, *cf* 21·4–13·9, M = 22·8%), and by its fewer gill-rakers (10 *cf* 12–15, mode 15).

From *S.* (*Sarg.*) *coulteri* it is distinguished, apart from differences in the pharyngeal bones, by its shorter pectoral fins (22·3–22·9% SL, *cf* 25·4–29·3, M = 27·3%), much shorter snout (31·8–33·7% head, *cf* 36·9–40·4, M = 38·7%), slightly shallower preorbital depth (18·6–19·3% head, *cf* 20·6–22·1, M = 21·4%), and somewhat longer lower jaw (44·2–46·6% head, *cf* 37·4–42·6, M = 39·6%).

Affinities. It is difficult to suggest any phylogenetic relationships for *S.* (*Sarg.*) *gracilis* within the *Sargochromis* assemblage. In part this is because virtually no anatomical information is available for the new species, and in part because it seems to share no uniquely derived features with any other member of the group. The characters which it does share with *S.* (*Sarg.*) *greenwoodi* and *S.* (*Sarg.*) *coulteri*, in particular those shared with the former species, appear to be plesiomorphic ones associated with the generalized type of pharyngeal jaws present in both taxa. For the moment *S.* (*Sarg.*) *gracilis* can only be considered a possible candidate for sister-species relationship with *S.* (*Sarg.*) *greenwoodi.* If that were established, the two species would then constitute a sister group to all other *Serranochromis* species. The relationships of *S.* (*Sarg.*) *coulteri,* because of its relatively derived pharyngeal dentition, would be with other members of the subgenus.

***SERRANOCHROMIS* (*SERRANOCHROMIS*) Regan, 1920**

For a description and diagnosis of the subgenus see Greenwood (1979: 299 *et seq.*).

Two species, *Serranochromis* (*Serranochromis*) *thumbergi* (Castelnau) and *S.* (*S.*) *macrocephalus* (Blgr) are represented in the Penrith collection. Several of the specimens were badly distorted in preservation, but it has been possible to identify them by using a combination of various and mutually exclusive characters. Because of their poor preservation no detailed descriptions of the species can be given. The material differs little from that described by Trewavas (1964) from other localities, but where differences were observed, or could be observed, these will be noted.

In the distribution maps published in her monograph, Trewavas (1964) records *S.* (*S.*) *thumbergi* and *S.* (*S.*) *robustus jallae* from the Cunene (*op. cit.*: fig. 26), and *S.* (*S.*) *macrocephalus*, with *S.* (*S.*) *angusticeps*, from a short, isolated and westward flowing river north of the Cunene (*op cit.* figs 27 & 28 for the species respectively). This river opens to the sea near the town of Mossamedes. Since the Angolan material which Trewavas lists for the two latter species (*op. cit.*: 34 & 40) bears only the locality 'Mossamedes', her indication of their occurrence near that town seems reasonable enough (as would, for the same reason, her record of *S.* (*S.*) *robustus jallae* in the same river). However, according to Dr Penrith (*in litt*)... 'A problem with some early collections, especially Ansorge's, has been the use of Mossamedes. This could refer to the town of that name; it could and usually did, refer to the district, a district that in the nineteenth century comprised most of southern Angola. Maps show two rivers flowing into the sea near Moçamedes, the Bero and the Giraul, and a third, the Curoca, entering the sea slightly further south. None of these rivers is perennial, and with the exception of some isolated stretches are dry for much of the year. Most older references to "Mossamedes" therefore probably refer to the Kunene river'.

The same doubt must affect the presumed localities for certain Angolan *S.* (*S.*) *robustus* specimens. These were also collected by Ansorge from 'Mossamedes', and on Penrith's arguments could have come from the Cunene river, thus casting doubt on Trewavas' record of the species in the small river north of the Cunene. Other *S.* (*S.*) *robustus* material collected by Ansorge, however, is from Donguena, and therefore is definitely attributable to the Cunene river system, as is the Hamburg Museum specimen (ZMH 1718) from Mülongo-Fürt. Possibly we should accept with reservation the presence of *S.* (*S.*) *robustus*, *S.* (*S.*) *macrocephalus* and *S.* (*S.*) *angusticeps* in the small northern river indicated on Trewavas' (1964) maps until their presence is confirmed by further collections.

No specimens identifiable as *S.* (*S.*) *angusticeps* are included in the new collection, but the identification of two Cunene river specimens, collected by Ladiges in 1959 (ZMH 1300 & 1307), as *S.* (*S.*) *angusticeps* can be confirmed.

***Serranochromis* (*Serranochromis*) *thumbergi* (Castel.)**

For the species as a whole, Trewavas (1964: 24 & 26) described the coloration of specimens preserved in alcohol. She noted that vertical markings on the body may be absent or, if present, are much fainter than the longitudinal ones, and are confined to the upper part of the body. Two of the four Cunene specimens (168–183 mm SL; all from the Matala Dam, Luceque) have the vertical bars predominating, while the two other fishes have the longitudinal midlateral stripe as the dominant component. In one of the latter specimens, both the vertical and horizontal markings are faint, and equally so.

The total vertebral counts (excluding the PU_1 and U_1 centra) in all four specimens is 36, comprising 18 abdominal and 18 caudal elements in three specimens, and 19 and 17 centra respectively in the fourth fish. These figures are in agreement with those given by Trewavas.

The identity of two *S.* (*S*). *thumbergi* specimens in the Hamburg Museum (ZMH 1719) was confirmed. Both were collected by Ladiges from the Cunene river at Capelongo, Angola (14° 55′S, 15° 06′E). In one, the horizontal markings of the colour pattern predominate, but in the other, the horizontal and longitudinal components are equally intense.

Serranochromis* (*Serranochromis*) *macrocephalus (Blgr)

Only one large specimen (160 mm SL; from Luceque) is represented in the collection, the remaining 21 individuals are much smaller (31–110 mm SL) and come from a number of different localities (see below, p. 230).

It is regrettable that the majority of small specimens are so badly distorted as to render them unsuitable for morphometric analysis. Little information is available on allometric and other growth changes in any *Serranochromis* species.

Total vertebral counts (excluding PU_1 and U_1) in the specimens radiographed, which included the largest and the smallest fish, are 32 (f11) and 33 (10), comprising 15 (f11) or 16 (f10) abdominal and 16 (f4), 17 (f13) or 18 (f4) caudal elements. Trewavas (1964: 29) gives the total counts in this species as 31–33, and the range for abdominal centra as 15 or 16; the only caudal count she records is 17 (all these figures are adjusted from Trewavas' original counts so as to exclude PU_1 and U_1 centra). The low number of abdominal vertebrae in *S. (S.) macrocephalus*, and hence the low total count, serves as a further feature distinguishing this species from the superficially similar *S.* (*S*). *robustus jallae.*

One of the specimens examined (from a locality 45 miles west of Ondurusu Falls) is unique amongst all the *Serranochromis* (*Serranochromis*) specimens in the collection in having anal sheath scales present (see p. 188 above).

Serranochromis (Serranochromis) angusticeps (Blgr) and ***S.* (*S.*) *robustus jallae*** (Blgr)

As noted earlier, neither of these species is represented in the new collection. However, the presence of both species in the Cunene river has been confirmed on the basis of specimens in the Hamburg Museum collections (see p. 189).

Zoogeographical considerations

Before considering what light the new material might throw on the zoogeography of the Cunene river fish fauna, attention must be given to four species which Poll (1967: 23) lists as occurring in that river. The species involved are *Haplochromis darlingi* (Blgr), *H. angolensis* (Steindachner), *H. frederici* (Castelnau) and *H. mellandi* (Blgr). The last named species has been discussed already in connection with the Cunene *Serranochromis* (*Sargochromis*) (p. 224).

The presence of *Haplochromis darlingi* (now *Pharyngochromis*; see Greenwood, 1979: 310), a species otherwise known only from the Zambezi, is based on Poll's redetermination of specimens first identified by Pellegrin (1936: 60) as *Pelmatochromis welwitschi.* Poll (*op. cit.*) also identified several more specimens from various Angolan rivers as *H. darlingi.* His

Study material and distribution records for *Serranochromis (Sargochromis)* species

Museum register number		Locality
BMNH; P=collection no.		
giardi–codringtoni complex		
1984.2.8:1		Cunene R., below Ruacana falls (17° 24′S, 14° 13′E).
1984.2.6:149	P 984	Cunene R., 45 miles west of Ondurusu falls (17° 03′, 13° 30′E).
coulteri:		
1984.2.6:150	P809	Cunene R., nr Cafu (16° 30′S, 15° 10′E).
1984.2.6:151	P1094	Cunene R., Matala dam at Luceque (14° 36′S, 15° 18′E).
1984.2.6:152	P1095	Cunene R., Matala dam at Luceque (14° 36′S, 15° 18′E).
1984.2.6:153	P1120	Locality unknown.
greenwoodi:		
1984.2.6:154		Cunene R., Matala dam at Luceque (14° 36′S, 15° 18′E).

Study material and distribution records for *Serranochromis* (*Serranochromis*) species

Museum register number		Locality
BMNH; P=collection no.		
thumbergi:		
1984.2.8:2	P1551	Cunene R., at Luceque (14° 40′S, 15° 07′E).
1984.2.8:3.	P1091	Cunene R., Matala dam at Luceque (14° 36′S, 15° 18′E).
1984.2.8:4	P1093	Cunene R., Matala dam at Luceque (14° 36′S, 15° 18′E).
1984.2.8:5	P1096	Cunene R., Matala dam at Luceque (14° 36′S, 15° 18′E).
macrocephalus:		
1984.2.8:6–12	P665	Cunene R., 45 miles west of Ondurusu falls (17° 03′, 13° 30′E).
1984.2.8:13–17	P669	Cunene R., 45 miles west of Ondurusu falls (17° 03′, 13° 30′E).
1984.2.8:18	P670	Cunene R., 45 miles west of Ondurusu falls (17° 03′, 13° 30′E).
1984.2.8:27	P899	Cunene R., Calueque (17° 16′S, 14° 30′E).
1984.2.8:19–20	P808	Cunene R., Calueque (17° 16′S, 14° 30′E).
1984.2.8:21	P1092	Cunene R., Matala dam at Luceque (14° 36′S, 15° 18′E).
1984.2.8:22–23	P1116	Cunene R., Chiatapu (14° 23′S, 15° 18′E).
1984.2.8:24–26	P1179	Cunene R., Jamba-ia-Homa (13° 46′S, 15° 30′E).

description of these fishes, in particular the presence of large anal spots in males, led me to express some doubts about their true identity (Greenwood, 1979: 311). Now, having examined some of Poll's material (from Lake Calundo; MCA: 163987–986), these doubts are reinforced. Certainly the specimens do resemble *Ph. darlingi* in some respects, but the anal fin markings are unlike those of Zambezi *Ph. darlingi*, while the lower pharyngeal bone and dentition in the Angolan fishes are, respectively, less well-developed and less molarized. Thus, at least until more is known about intraspecific variation in Zambezi *darlingi*, and until the live coloration of specimens from Angola and elsewhere is recorded, I would defer any inclusion of *Ph. darlingi* amongst the haplochromine species of Angola. The Angolan '*darlingi*', I suspect, probably represents an undescribed species distinct from that in the Zambezi, and one whose phylogenetic and hence generic relationships are at present indeterminable.

Poll's inclusion of *Haplochromis angolensis* in the Cunene fauna stems from Boulenger's (1915: 409) identification of three specimens from Mossamedes as that species. It is these specimens which Bell-Cross (1975: 451) reidentified as *Haplochromis giardi*, and which are discussed on page 220 above. The single type specimen of Steindachner's *angolensis* is now lost (see Bell-Cross, 1975: 426) and the true identity of the taxon is unlikely to be determined because the original description is totally inadequate for that purpose. The inclusion of *angolensis* in the Cunene faunal list would, therefore, seem to be rendered null and void. As a result of Bell-Cross' reidentification of the specimens involved, the record for *H. angolensis* should be replaced by one for *Serranochromis* (*Sargochromis*) *giardi*. But, as discussed on p. 224 above, there are certain doubts about the specific identity of *giardi*-like fishes in the Cunene.

The record for *Haplochromis frederici* (now *Serranochromis* [*Sargochromis*] *greenwoodi*, see Bell-Cross, 1975, and Greenwood, 1979) was presumably based on Ladiges' (1964: 268) identification of four fishes from Capelongo as *H. frederici*. I have examined these specimens (ZMH 1722), and find that two (190 and 122 mm SL) should be referred to the *Serranochromis* (*Sargochromis*) *giardi–codringtoni* complex (see p. 222) and that the other two (132 and 76 mm SL) can be referred, provisionally, to *S.* (*Sarg.*) *coulteri* (Bell-Cross). Interestingly, *S.* (*Sarg.*) *greenwoodi* is present amongst the new Cunene material (see p. 224).

The new cichlid material from the Cunene river, and the taxonomic changes which it has necessitated, throw very little fresh light on the zoogeographical relationships of the river's haplochromine fauna (but see, Appendix II).

The species of *Serranochromis* (*Serranochromis*) occurring in the Cunene also occur in the Upper Zambezi system (including the Okovango river), the Kafue, the Upper Zaire drainage, and in the other Angolan rivers. At the species, but not the subspecies-level, one taxon *S.* (*S.*) *robustus* extends to Lake Malawi and the Shire river (see Trewavas, 1964 and 1973; Poll, 1967).

Because of the confused species-level taxonomy of *Serranochromis* (*Sargochromis*), little zoogeographical information can be derived from the species of that subgenus in the Cunene. It seems likely, nevertheless, that their relationships are with taxa from the Zambezi and Kafue systems, the Cunene fishes being either conspecifics or, if specifically distinct, their vicariant counterparts.

The genus *Pseudocrenilabrus* has an extraordinarily wide distribution in Africa (Nile, Lakes Victoria, Edward, George and Malawi, the Zambezi, Limpopo and Zaire basins, various Angolan rivers, the Okavango and Orange rivers, and the rivers of Natal and Kwazulu). Once again, inadequate species-level taxonomy precludes any fine zoogeographical analysis (see p. 214). The Cunene and other populations of *Pseudocrenilabrus* appear to be referable to *Ps. philander*, a species with a wider, but more southerly distribution than its congener *Ps. multicolor* which is confined to the Nile, Lakes Victoria, Edward, George and to streams and small lakes in Uganda. The Cunene *Pseudocrenilabrus* species is certainly quite distinct from *Ps. ventralis*, a species endemic to the Zaire river (Nichols, 1928).

That several of the Cunene and other Angolan haplochromines previously classified in the genus *Haplochromis* are now referred to *Thoracochromis* (p. 189) is possibly of some biogeographical significance. *Thoracochromis* has a wide distribution encompassing the Nile (including Lake Albert), Lake Turkana, Lakes Edward and George, Lake Mweru, and the lower Zaire drainage system (see Greenwood, 1979: 293). It has not so far been found in the Zambezi. The two Cunene species, *Th. buysi* and *Th. albolabris*, are both endemic to that system; unfortunately their phyletic relationships cannot yet be determined.

Morphologically, *Th. buysi* is a generalized species, and could well be the local, that is vicariant member of a group including at least two other Angolan taxa, *Th. lucullae* and *Th. schwetzi.* There are indications from the material I have examined that other species will eventually be added to the group.

Thoracochromis albolabris, in sharp contrast, is a highly derived taxon (see p. 204) whose specialized features, being autapomorphic ones, do not help in establishing its relationships within the genus. Certainly there are no characters indicative of affinity with any Zairean taxa, nor with its Angolan congeners. Indeed, the only relationship suggested is with *Melanochromis labrosus* of Lake Malawi (see p. 205). That possibility cannot be elaborated further until more is known about the anatomy and osteology of *M. labrosus.*

Finally, there is *Orthochromis machadoi*, another endemic species, and a member of another genus with Zairean connections (see Greenwood, 1979: 297). Unlike *Thoracochromis*, *Orthochromis* is otherwise confined to the Upper Zaire system (extending that drainage, in an historical context, to include the Malagarazi river which now empties into Lake Tanganyika).

Orthochromis machadoi is the least derived member of the genus, and thus cannot be linked, as a sister-species, with any of its congeners. Its colour pattern suggests a possible affinity with *O. malagaraziensis* of the Malagarazi river, Tanzania (see Greenwood, 1979: 298), but the value of that character for establishing a true phyletic relationship is still untested.

In brief, and on a broad scale, it seems that the new collection corroborates earlier suggestions of the Cunene cichlid fauna's affinities with those of the Zambezi and Zaire systems (Trewavas, 1964 & 1973; Bell-Cross, 1975; Roberts, 1975). Any finer resolution of those affinities will depend on the acquisition of many more data leading to greater precision in establishing interspecific relationships. For the moment it is much easier to recognise differences, that is endemicity, than it is to assess phylogenetic affinities.

Any remarks made about levels of endemicity for particular rivers in Angola must perforce be cautious ones since the area is still poorly collected. The situation is also complicated by the absence of precise locality data for some apparently 'good' species currently represented by one or a few specimens. From the information now available, the Cunene has at least four endemic haplochromine species, namely, *Orthochromis machadoi*, *Serranochromis* (*Sargochromis*) *coulteri*, *Thoracochromis buysi* and *Th. albolabris*, and there are indications of two or possibly three other endemic species as well. Even without the inclusion of these undescribed taxa, the Cunene has the highest number of endemic haplochromines for any Angolan river (see Poll, 1967; Trewavas, 1973).

Several difficulties are encountered when attempting to compare the Cunene haplochromine fauna with that of other rivers in Angola, in particular those which flow westward and empty directly into the Atlantic. In part these problems stem from the inadequacy of existing collections, and in part from the poor documentation of earlier collections. For example, as species occurring in westward flowing rivers, *other than the Cunene*, Poll (1967: 23) lists, under the generic name *Haplochromis*, the taxa *acuticeps*, *fasciatus*, *humilis*, *lucullae*, *multiocellatus* and *welwitschi.* The type locality for *acuticeps* is recorded only as Angola, and the species has not since been identified in material from any westward flowing river. Likewise, *humilis*, known from the holotype only, has not been recorded since its original description; again, the type locality was given merely as Angola. *Haplochromic fasciatus* (now *Thoracochromis*) does not appear to have been collected in any westward flowing Angolan river (*pace* Poll's reference to Regan [1922], who cites its distribution only as 'Lower Congo'). There are doubts about the identity of certain specimens referred to the species by Regan (see Greenwood, 1979: 293), but the types are from the lower Zaire drainage.

Poll's (*op. cit.*) listing of *Haplochromis welwitschi* in western rivers other than the Cunene is probably attributable to uncertainty about the exact provenance of the holotype, for long the only known example of the species. It seems likely that, apart from Poll's specimens taken in tributaries of the Cubango river (Zaire drainage) and other Angolan rivers flowing into the Zaire system, the only other recorded locality for the species is the Cunene river (see Appendix II).

Finally, there is the problem of *Haplochromis angolensis.* This is discussed fully on p. 220. In brief, the specimens to which Poll refers were misidentified by Boulenger (1915), and anyhow came from the Cunene drainage and not one of the other westward flowing rivers in which Poll records the species' presence.

Thus, in effect, Poll's list of five haplochromine species in western rivers other than the Cunene is reduced to two, *lucullae* and *multiocellatus*; these taxa may be referred to as 'small haplochromines' in contradistinction to those whose individuals reach a much larger adult size (that is, species of *Serranochromis*). The 'small haplochromines' are represented in the Cunene by three endemics, *Thoracochromis buysi*, *Th. albolabris* and *Orthochromis machadoi*, and the non-endemic *Pseudocrenilabrus philander.* Using adult size as a criterion, the non-endemic *Chetia welwitschi* (see Appendix II) should also be included as a Cunene 'small haplochromine'. If what appear to be two undescribed species (so far represented by inadequate samples) are also included, the total number of Cunene 'small haplochromine' species is seven, five more than in any of the other westward flowing rivers of Angola.

For the 'large haplochromines' in the other rivers, Poll (1967: 23) lists a total of five taxa, *viz* four species of *Serranochromis* (which would now be referred to the nominate subgenus of that taxon), and *Haplochromis mellandi* (now referred to the subgenus *Sargochromis* of *Serranochromis*). The four *Serranochromis* (*Serranochromis*) species also occur in the Cunene (see p. 228 above). Because of the confused situation surrounding the taxonomy of Angolan *Serranochromis* (*Sargochromis*) species it is not certain whether *S.* (*Sarg.*) *mellandi* occurs in the Cunene, or, indeed, whether it is present in Angola at all. A *mellandi*-like taxon is present in some Angolan rivers, and may be in the Cunene as well. It is possible that five *S.* (*Sargochromis*) taxa occur in that river, namely a *giardi*-like and a *mellandi*-like species, together with *S.* (*Sarg.*) *coulteri*, a species close to, if not conspecific with *S.* (*Sarg.*) *greenwoodi* and *S.* (*Sarg.*) *gracilis.*

Thus, from the data currently available, the Cunene haplochromine fauna, in terms of species numbers, is probably richer than that of all the other westward flowing rivers combined, and also richer than that of those rivers which ultimately flow into the Upper Zaire river basin.

Indeed, at the species level, haplochromine diversity in the Cunene is higher than in the Zambezi-Kafue system, a situation attributable mainly to the greater number of 'small haplochromine' species present in the Cunene, three of which are members of Zairean genera (*Thoracochromis* and *Orthochromis*) not represented in the Zambezi and Kafue rivers.

In conclusion it can be noted that the genus *Pseudocrenilabrus* is present in the Cunene, but not in other westward flowing rivers of Angola, whilst *Hemichromis* which does occur in those rivers (Poll, 1967) is apparently absent from the Cunene. The reverse pattern to that of *Hemichromis* holds for *Orthrochromis*, a genus represented in the Cunene by the endemic *O. machadoi*, but one which seemingly is absent from other Angolan rivers emptying directly into the Atlantic. Possibly these paradoxes could be resolved if more was known about the ecological requirements of the species involved.

Appendix I

The generic status of various Angolan species referred to *Haplochromis* by Regan (1922), Poll (1967), Trewavas (1973) and Bell-Cross (1975)

Four species in this category have now been placed in the genus *Thoracochromis*, see pp. 189–206 above. The generic status of certain other species was reviewed in Greenwood

(1979). There, reasons were given for transferring *H. thysi* Poll (1967) and all the 'large *Haplochromis*' species revised by Bell-Cross (1975) to the subgenus *Sargochromis* of *Serranochromis*. Also in that paper, *H. machadoi* Poll (1967) was recognised as an *Orthochromis* species (see also p. 206 above).

The generic status of the other Angolan '*Haplochromis*' species remains uncertain.

Haplochromis humilis (Steindachner), 1866, recorded only as being from Angola, is not currently available for reexamination (see p. 189). Bell-Cross' (1975: 426) comments, coupled with Steindachner's original description and accompanying figure, suggest that the specimen should probably be referred to a species of *Serranochromis* (*Sargochromis*).

The type of *H. angolensis* (Steindachner), 1865 is lost (see Bell-Cross, 1975: 426); the original description is so inadequate that the type specimen's identity cannot be determined at either generic or specific levels.

The type and only specimen of *Haplochromis multiocellatus* Blgr, 1913 has a gradual size-change of scales in the transition area between chest and belly squamation. Such a pattern would exclude the species from *Thoracochromis* (see Greenwood, 1979: 290), a genus with which it shares no other diagnostic features either. That the type appears to have true anal ocelli of the kind found in *Astatotilapia* and in the majority of Lake Victoria haplochromines (see Greenwood, 1979: 274–5), would also seem to argue against its inclusion in *Thoracochromis*. However, details of anal fin markings are difficult to ascertain in preserved specimens, and the absence of true ocelli in all *Thoracochromis* species has yet to be established on the basis of fresh or live material. Thus, the generic status of '*Haplochromis*' *multiocellatus* must remain undetermined, except in so far as it cannot be referred to the genera *Haplochromis*, *Thoracochromis* or *Serranochromis* as defined by Greenwood (1979). At a lower taxonomic level, it should be recalled that Trewavas (1973: 31) believes the taxon to be a junior synonym of '*H*' *acuticeps* (whose generic status is, at least for the moment, also uncertain (see above, p. 190)).

Haplochromis welwitschi (Blgr) 1898, is discussed in Appendix II.

Appendix II

The generic status of *Pelmatochromis welwitschi* Blgr, 1898

Surprisingly, this species has never been formally transferred to any other haplochromine genus, despite the fact that it clearly is not a member of the genus *Pelmatochromis* as currently defined, and despite its obvious membership of the genus *Haplochromis* as defined by Regan (1920 & 1922). It has, however, been referred to as *Haplochromis welwitschi* by several workers, notably Poll (1967), Trewavas (1964) and Bell-Cross (1975).

When reviewing the generic status of fluviatile haplochromine species (Greenwood, 1979: 310 & 313), I commented on the possible generic affinities of *P. welwitschi*, particularly in the light of Trewavas' (1974: 9; fig. 1) suggestion that it might be related to *Serranochromis* (Greenwood, 1979: 306).

At that time I considered whether the species might be included in the genus *Chetia* Trewavas (1961) but expressed reservations about its formal transfer to that taxon until further material could be studied. Having now had the opportunity to examine specimens from Angola, kindly lent to me by the MRAC, I would withdraw those reservations.

My reasons for doing so are based on *Chetia flaviventris*, type species of the genus, sharing with *P. welwitschi* a number of character combinations which neither genus shares with other haplochromine taxa. These include dental characters, features of the squamation pattern, vertebral numbers, and the type of spotting on the anal fin of male fishes. The recently described *Chetia mola* (see Balon & Stewart, 1983) also shares these features, differing only in its hypertrophied pharyngeal jaws and dentition, and in correlated modifications to the neurocranial apophysis for the upper pharyngeal bones.

The entirely unicuspid oral dentition of available *welwitschi* specimens is like that in larger

Chetia flaviventris specimens. In *C. flaviventris*, the unicuspid outer row teeth appear in specimens of a very small size (see Trewavas, 1961); since none of the *welwitschi* material is less than 100 mm SL, it is not possible to check whether this species, too, shows a similar precocity in dental ontogeny. Neither *welwitschi* nor *C. flaviventris* has enlarged and serially displaced median teeth in the inner premaxillary tooth row (see p. 216).

Apart from the last 1 to 4 scales in the upper lateral-line series, all the scales in that row of both species are each separated from the dorsal fin base by at least one small and two large scales of equal size, comparable in that respect with the pored scales below them.

The lower pharyngeal bone in *C. flaviventris* and in *welwitschi* is fine and relatively narrow, with long and delicate (*welwitschi*) or relatively delicate posterior horns (*cf* Fig. 20 with fig. 19 in Greenwood, 1979). None of the median row teeth in *welwitschi* is much coarser than the teeth situated laterally in the dental field, but in *C. flaviventris* some median teeth are slightly coarser than those elsewhere on the bone. The morphology of the pharyngeal teeth is similar in both species; only those teeth in the posterior half of the dental field have a well-marked shoulder or a distinct minor cusp, the others being essentially unicuspid with a sharp and oblique crown.

Like *C. flaviventris*, *P. welwitschi* has numerous spots on the anal fin of male fishes. In the holotype of *P. welwitschi*, now faded, there are about 8–10 spots arranged in a short upper and a longer lower row; the MRAC specimens examined have an estimated 13–15 spots, in several irregular rows, scattered over the greater part of the fin, but these fishes are larger than the holotype (see p. 237 below).

Finally, both *C. flaviventris* and *welwitschi*, when compared with all the other fluviatile haplochromine species except *Serranochromis*, show a tendency towards an increase in the number of abdominal vertebrae (see Greenwood, 1979). The three *welwitschi* specimens all have 14 or 15 abdominal elements, most of the *C. flaviventris* examined have 15, although 14 were counted in one.

It must be stressed that none of the distinctive characters shared by *Chetia flaviventris* and *P. welwitschi* is uniquely synapomorphic for the two species (see Greenwood, 1979: 308–310

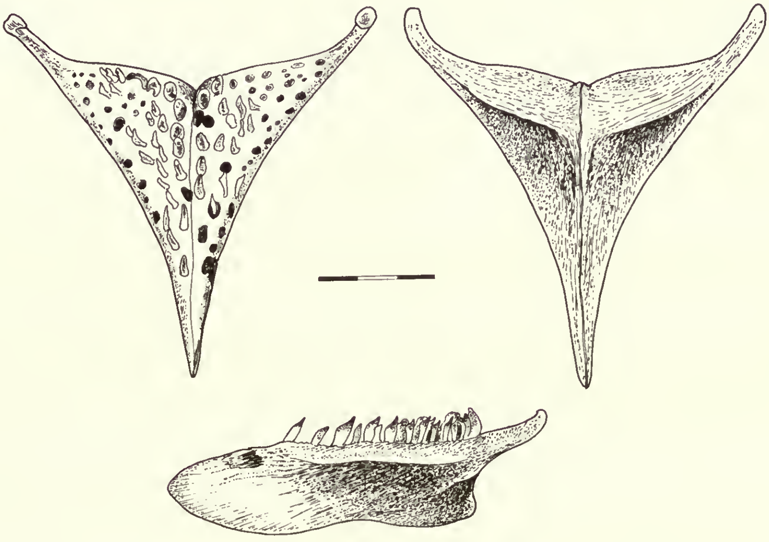

Fig. 20 *Chetia welwitschi*. Lower pharyngeal bone. Numerous teeth are missing, but their sites of attachment are indicated. Scale in mm.

for further discussion). Taken together, however, the various characters appear to be shared only by these two species and *C. mola*. Since none has any detectable feature or features shared uniquely by it and any other genus, it would seem reasonable to consider them congeneric until such times as their implied monophyly can be refuted. There would certainly seem to be no grounds for recognising *welwitschi* as representing a distinct lineage, and thus a distinct genus.

Chetia welwitschi (Blgr) 1898

SYNONYMY. *Pelmatochromis welwitschi* Boulenger, 1898. *Proc. zool. Soc. London*: 149, pl. xix; *idem*, 1915. *Cat. Afr. Fw. Fishes*, **3**: 397, fig. 268.

Haplochromis welwitschi: Trewavas, 1964. *Annls Mus. r. Congo Belg*, Ser. 8vo, Zool. no. 25: 1–58; Poll, 1967. *Publiçacões cult. Co. Diam. Angola* no. 75: 1–381; Bell-Cross. 1975. *Occ. Pap. natn. Mus. Rhod.* ser. B. **5** (7): 405–464; Greenwood, 1979. *Bull. Br. Mus. nat. Hist.* (Zool.) **35** (4): 265–322.

DESCRIPTION. Poll (1967: 307–309; fig. 149) gives a detailed account of the Angolan material he examined. The table and comments below refer only to the holotype (BMNH 1864.7.13: 62) and the two Angolan specimens from Sanguenque Uembe Cûanaa, Angola, loaned by the MRAC (154779–780), which were not included in Poll's (1967) redescription of the species.

In three morphometric features (smaller eye, deeper preorbital and longer lower jaw), the MRAC specimens differ slightly from the holotype, but these discrepancies could be due to the larger size of the former. There is, however, a marked discordance in caudal peduncle length when Poll's (1967) figures for other material are compared with those obtained from the specimens described above. Poll gives the caudal peduncle length as 30·0 and 32·6% of the standard length; one can only conclude that these figures are typographical errors.

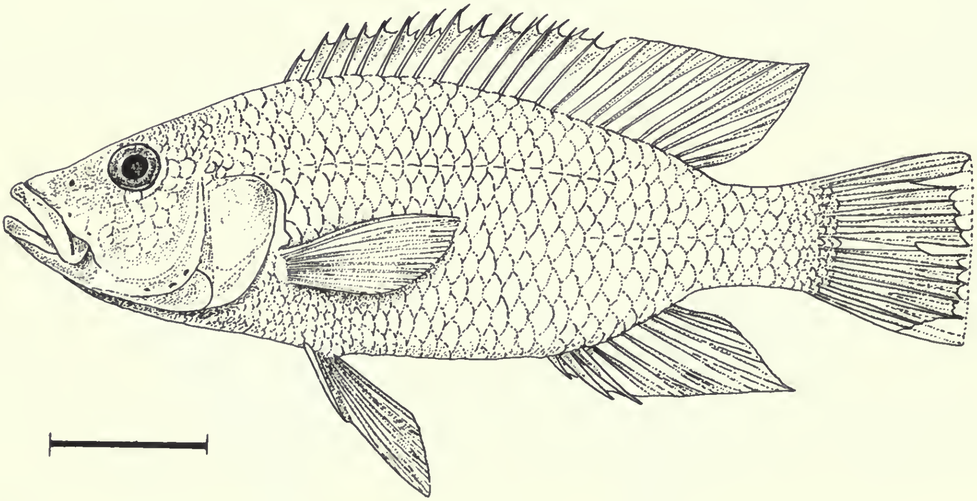

Fig. 21 *Chetia welwitschi* (Blgr). Holotype; after Boulenger (1915). Drawn by G. J. Howes. Scale = 20 mm.

There are 34 scales in the lateral-line series of the holotype, and 32 in the MRAC specimens. In the original description, Boulenger (1898) gives a count of 32 for the type, but this was changed to 33 in his 1915 description of the species. No anal sheath scales are present in the MRAC fishes, but a few scattered scales, on both sides of the fin, are preserved in the holotype. None was found in the type and two paratypes of *Chetia flaviventris* I examined.

	Holotype BMNH:1864.7.13:62	MRAC Specimens 154779–780	
Standard length	102·0	126·0	146·0
Depth of body*	33·3	34·1	34·2
Length of head*	32·3	34·1	34·2
Preorbital bone depth†	24·3	20·9	21·0
Least interorbital width†	21·2	23·3	22·0
Snout length†	36·3	34·9	34·0
Snout length/breadth	1·1	1·0	0·9
Eye diameter†	22·8	18·6	20·0
Cheek depth†	33·3	32·6	32·0
Lower jaw length†	42·5	47·1	48·0
Lower jaw length/breadth	1·7	1·8	2·0
Caudal peduncle length/depth	18·6	17·0	17·5
Caudal peduncle length/breadth	1·4	1·5	1·5
Length of premaxillary ascend. processes†	33·0	30·2	30·0
Pectoral fin length*	18·1	20·6	20·5
†	56·0	60·5	60·0

* = percentage of standard length; † = percentage of head length

The holotype of *C. welwitschi* has 9 short and relatively stout gill-rakers on the lower part of the first gill-arch; there are 9 rakers in one of the MRAC specimens, and 11 in the other. Microbranchiospines are present in all three fishes, but are smaller and less obvious in the holotype.

Many outer row teeth are missing in the holotype, but I would estimate that about 40 were once present in the premaxilla. There are about 56 premaxillary teeth in the MRAC specimens (Poll [1967] gives a count of 68 in the two fishes he examined).

The holotype has 30 vertebrae (excluding the fused PU_1 and U_1 centra), comprising 15 abdominal and 15 caudal elements; the two other specimens both have 29, 14 of which are abdominal, and 15 are caudal elements. In *Chetia flaviventris* the counts are 30–32, mode 31, comprising 14 or 15 (mode 15) abdominal, and 15–17 (modes 16 and 17) caudal centra. Hypurals 1 and 2, and 3 and 4 are apparently fused in the MRAC specimens radiographed; in the holotype all are free, but 3 and 4 are closely apposed. All hypurals are free in the *Chetia flaviventris* material radiographed.

The pharyngeal apophysis of *C. welwitschi* holotype is of the *Haplochromis*-type, and is broad, with a laterally expansive contribution from the parasphenoid; its structure was not examined in the MRAC material. No information is available about the vertebral apophysis for the *retractor arcuum branchialis* muscle.

All three specimens are males and, apparently, are adult. The 146 mm SL fish is sexually active. In none does the first pelvic ray extend posteriorly beyond the anus. This ray in the 146 mm specimen is distinctly longer than the 2nd ray, but it is not filamentous; in the two smaller fishes, the first ray is but slightly longer than the second.

The occurrence and pattern of the numerous anal spots is described above (p. 235). Poll's drawing (1967: fig. 149) of another Angolan specimen shows, in contrast, only three or four spots confined to the posterior part of the soft anal fin. This may be the result of an artist's error stemming from the extreme difficulty one experiences in arranging the lighting to reveal such faintly pigmented areas.

There is some uncertainty about the type locality of *Chetia welwitschi*. Originally recorded as being collected by Welwitsch from Fluilla, Angola (Boulenger, 1898), it was later thought that Fluilla had been a misspelling of Huilla, a town and district in the south-western part of the country (Bell-Cross, 1975: 427). If that is so, then the holotype would be from the Cunene drainage. With the addition of Poll's material, the range of *C. welwitschi* is now extended to include the Zaire drainage system as well (Poll, 1967: 307).

If the generic placement of *P. welwitschi* is correct, then it is the only Angolan haplochromine, except *Pseudocrenilabrus philander*, belonging to a taxon also occurring in the Limpopo drainage (the type material of *Chetia flaviventris* is from a dam on the Sterkstroom river, a tributary of the Crocodile). That remark is made, of course, on the assumption that the specimens Poll identified as *Haplochromis darlingi* are not referable to the genus *Pharyngochromis*, the genus in which *H. darlingi* is now placed (Greenwood, 1979: 310).

Neither the inclusion of *Pelmatochromis welwitschi* in *Chetia*, nor the discovery of *C. mola*, provide any information on the phyletic relationships of the genus. As Trewavas (1964) suggested, its relationships would seem to be with the *Serranochromis* generic complex, but the characters on which that suggestion was made are still of unproven value in a truly phylogenetic scheme of classification (Greenwood, 1979: 309).

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British Museum (Natural History)

Tilapiine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

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Notes on testate amoebae (Protozoa: Rhizopoda) from Lake Vlasina, Yugoslavia

Colin G. Ogden

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

The morphology of some testate amoebae from Lake Vlasina, Yugoslavia has been reported in an earlier work (Ogden & Živković, 1983). This present study extends the survey to include recently collected specimens, some of which have already been used (Ogden, 1983*a*) in a reappraisal of the genus *Pontigulasia.* The author was fortunate to be guided on his visit in September, 1982, by Dr A. Živković who had collected the samples for the earlier work. Two contrasting sites were sampled, one at the southern extremity of this artificially created lake and the other at the northern. The southern site was an area of damp to wet pasture, with small ponds or pools scattered across it at intervals. It was one of several similar level expanses of land consisting of mixed grasses and patches of *Sphagnum* bordering the lake margin, used for grazing but possibly flooded or waterlogged in winter. The northern site was a small triangular inlet, which appeared to be in the process of being naturally reclaimed. It was covered with a floating mass of vegetation, including tall coarse grasses and small shrubs, but being mainly a platform of *Sphagnum.* It was possible to walk over the surface with care, but at each step water oozed up from below, the whole being buoyant and unsteady. The level of the lake was quite low during the visit, which was clearly seen from the water level marks around the shoreline, reflecting the end of a long dry summer. The large floating masses of peat which appeared on the lake surface after the initial flooding, described by Milovanović & Živković (1956), are now stranded well above the normal level of the lake. One such mass was seen straddled across the water course of a small stream as a solid block about 7 m high and 15 m long.

The main purpose of this study was to look particularly for specimens belonging to the family Difflugiidae, and to compare the organic cement patterns found in species of *Difflugia* with those already described (Ogden, 1983*b*) from sites in the British Isles. Such a comparison was considered to be a reasonable test of the validity of these patterns as a good taxonomic character. Nevertheless, several examples of other species of testate amoebae were examined and compared with those described earlier by the author. The samples were rich in specimens, and the numbers examined here and elsewhere (Ogden, 1983*a*) represent only a small proportion of those present.

Materials and methods

Samples of *Sphagnum* moss and water plants were collected from several points at each site. There was no apparent difference between samples taken over a large area at one site, but there were a few differences between the two sites. Individual specimens were extracted from the samples as being representative of the population, and animals described are a selection of those present. They were examined optically either by Nomarski interference or bright-field illumination, and by scanning electron microscopy. Preparative techniques for scanning electron microscopy have been described elsewhere (Ogden, 1983*b*), treated specimens were examined in either a Cambridge Stereoscan S180 or an Hitachi S800 microscope.

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Systematic section

An alphabetical arrangement has been adopted for both genera and the species in each genus. The numbers given for specimens measured refer to those which were examined in detail, and descriptions are included for those specimens which have not been the subject of earlier studies. When animals are found to be similar to a previous description that reference is quoted.

Arcella arenaria Greeff, 1866

One specimen examined: diameter of shell 99 μm, depth 30 μm, diameter of aperture 16 μm, similar to Plate 1, Ogden & Hedley, 1980.

Arcella discoides Ehrenberg, 1843

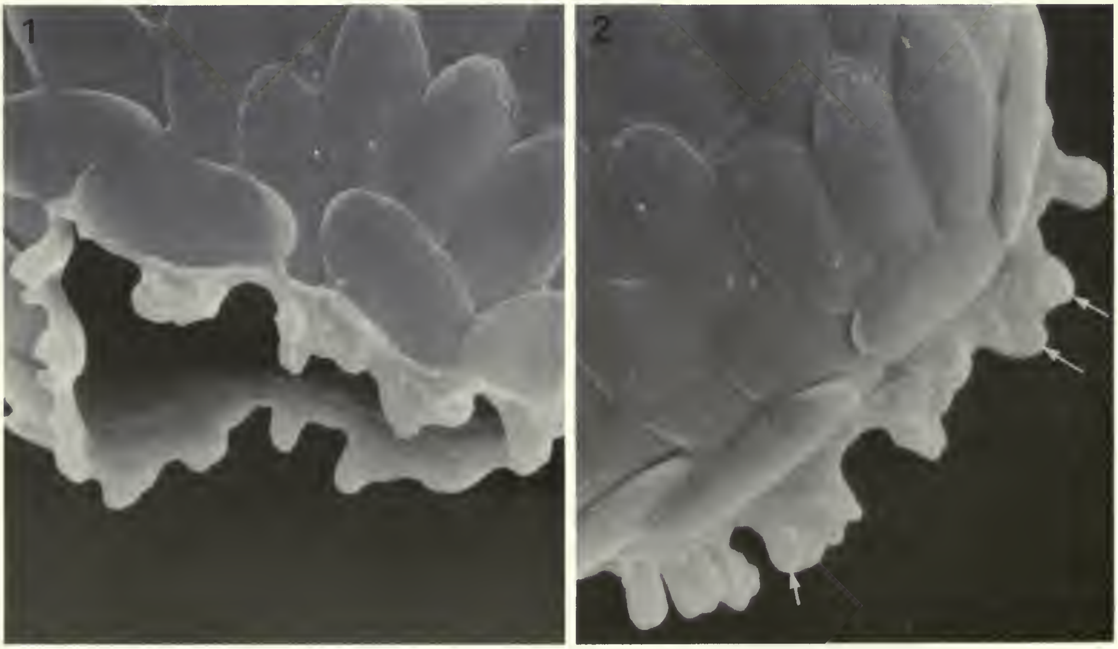
One specimen examined: diameter of shell 114 μm, depth 34 μm, diameter of aperture 46 μm, similar to Plate 7, Ogden & Hedley, 1980.

Arcella rotundata var. ***stenostoma*** Deflandre, 1928

Four specimens examined: diameter of shell 52–61 μm, depth 33–36 μm, diameter of aperture 12–14 μm. The specimens agree with the original description given by Deflandre (1928), except that the domed region was covered with small regularly spaced angular facets. Observations on clonal cultures of *Arcella vulgaris* led Ogden (1984) to suggest that this feature was unreliable as a specific character and it is treated as such here.

Assulina muscorum Greeff, 1888

One specimen examined: shell length 53 μm, breadth 31 μm, diameter of aperture 11 μm. This specimen agrees well with the description of Ogden & Hedley (1980) and Ogden (1981). It would appear from the detail shown in Figs 1 & 2 that small shell plates may be incorporated in the organic cement which characteristically surrounds the aperture.



Figs 1 & 2 *Assulina muscorum:* Two views of the aperture to illustrate the organic cement margin, with possibly small shell plates (arrowed) incorporated ×6000 and ×7000.

Centropyxis aerophila Deflandre, 1929

Five specimens examined: length of shell 54–70 μm, breadth 37–60 μm, depth 27–43 μm, diameter of aperture 21–35 μm, similar to Plate 13, Ogden & Hedley, 1980.

Centropyxis cassis (Wallich, 1864)

Two specimens examined: length of shell 108 & 122 μm, breadth 84 & 98 μm, depth 61 μm, diameter of aperture 53 & 49 μm, similar to Plate 14, Ogden & Hedley, 1980.

Centropyxis hirsuta Deflandre, 1929

Two specimens examined: length of shell 86 & 88 μm, breadth 51 & 73 μm, depth 40 & 42 μm, diameter of aperture 27 & 31 μm, similar to Plate 18, Ogden & Hedley, 1980.

Centropyxis platystoma Penard, 1890

Two specimens examined: length of shell 61 & 75 μm, breadth 33 & 36 μm, depth 28 & 30 μm, diameter of aperture 22 μm, similar to Plate 19, Ogden & Hedley, 1980.

Cyclopyxis kahli (Deflandre, 1929)

One specimen examined: diameter of shell 91 μm, depth 62 μm, diameter of aperture 24 μm, similar to Plate 24, Ogden & Hedley, 1980.

Cyphoderia ampulla (Ehrenberg, 1840)

Three specimens examined: length of shell 87–109 μm, breadth 39–55 μm, diameter of aperture 15–16 μm, similar to Plate 94, Ogden & Hedley, 1980.

Cyphoderia laevis Penard, 1902

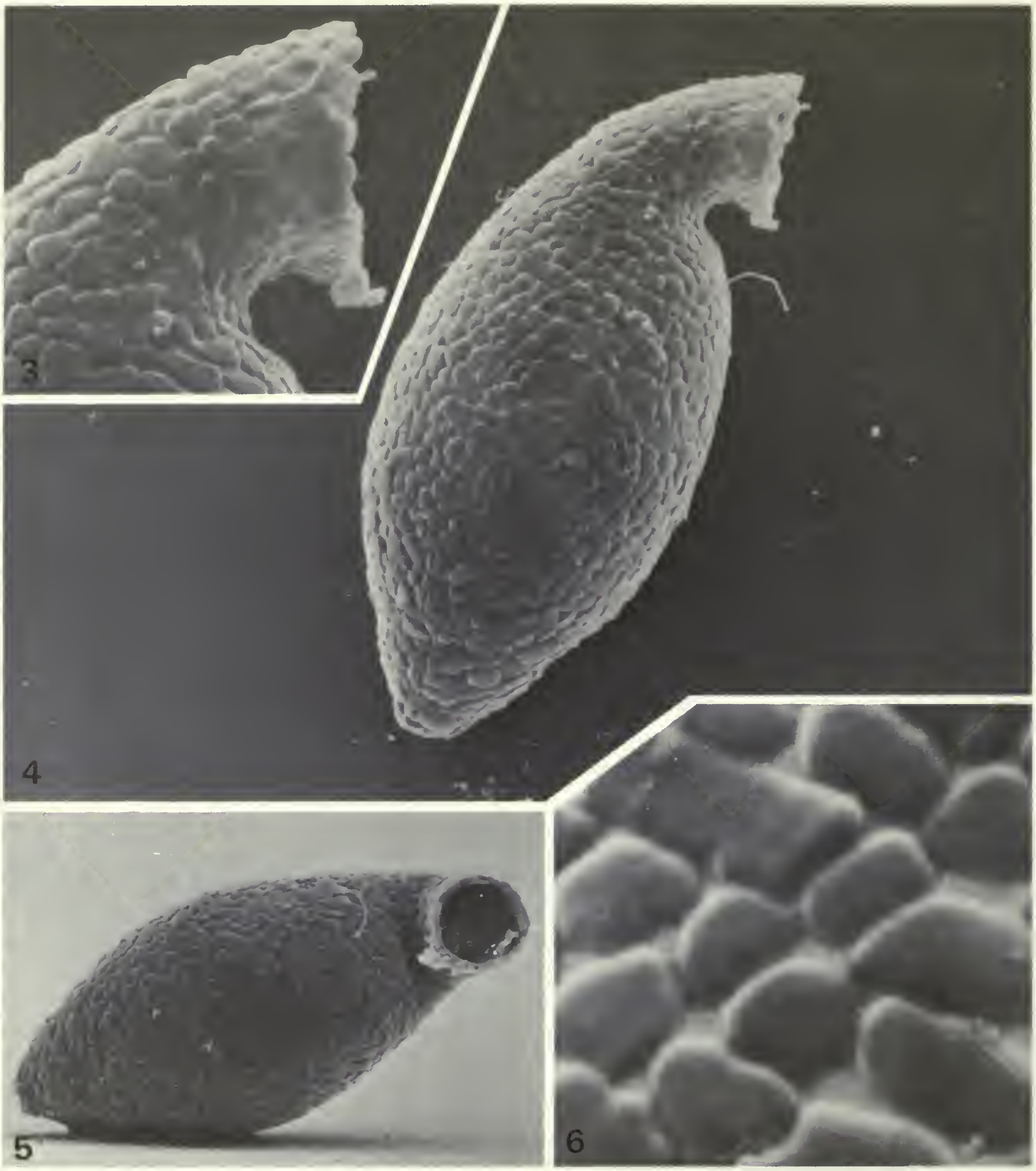
DESCRIPTION. The shell is colourless, retort-shaped and circular in cross section, being widest at about the mid-point and tapering to both extremities (Figs 3 & 5). A distinct neck is formed by the sharp curvature of the shell towards the aperture (Fig. 4). It is composed of oval shell plates which are irregular in outline and size, with the occasional elongate plate scattered amongst them (Fig. 6). An apparently structureless organic cement binds these plates together without any overlapping. The aperture is circular (Fig. 5) and has an even margin composed of small plates (Fig. 3).

MEASUREMENTS (in μm). Based on one specimen: length of shell 64, breadth 27, diameter of aperture 9.

REMARKS. This specimen is similar in size to those described by Penard (1902). It differs from his description because he stated that the curvature of the neck was hardly distinguishable from the general outline of the shell, whereas in the present specimen the shell has a distinct neck. Nevertheless, the shell plates are small and irregular in both size and distribution, which is in agreement with the original description. In the absence of other animals, the present specimen is considered to be conspecific with *C. laevis.*

Difflugia acuminata Ehrenberg, 1838

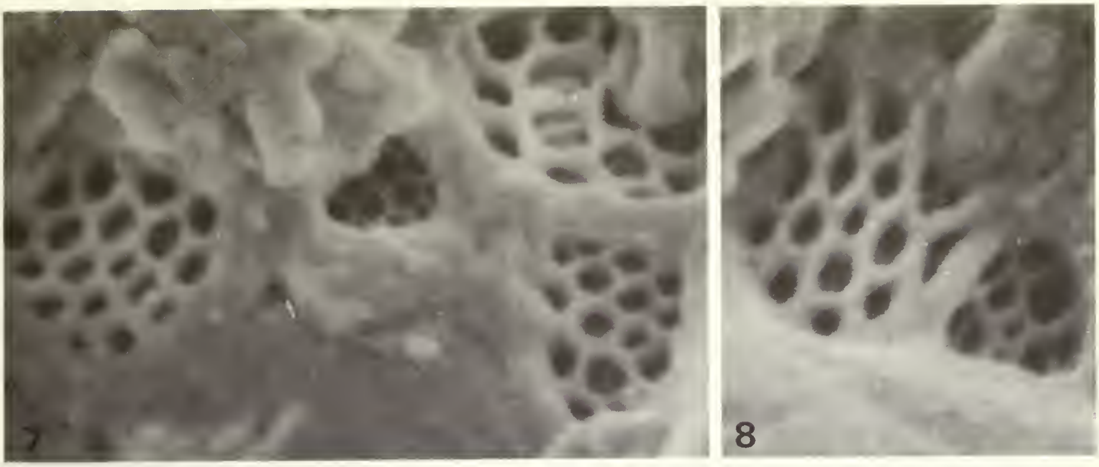
Four specimens examined: body length 228–274 μm, breadth 85–106 μm, diameter of aperture 37–46 μm, similar to Figs 3, 8 & 9, Ogden, 1979*a*. The distinctive organic cement pattern that distinguishes this species is shown in Figs 7 & 8.



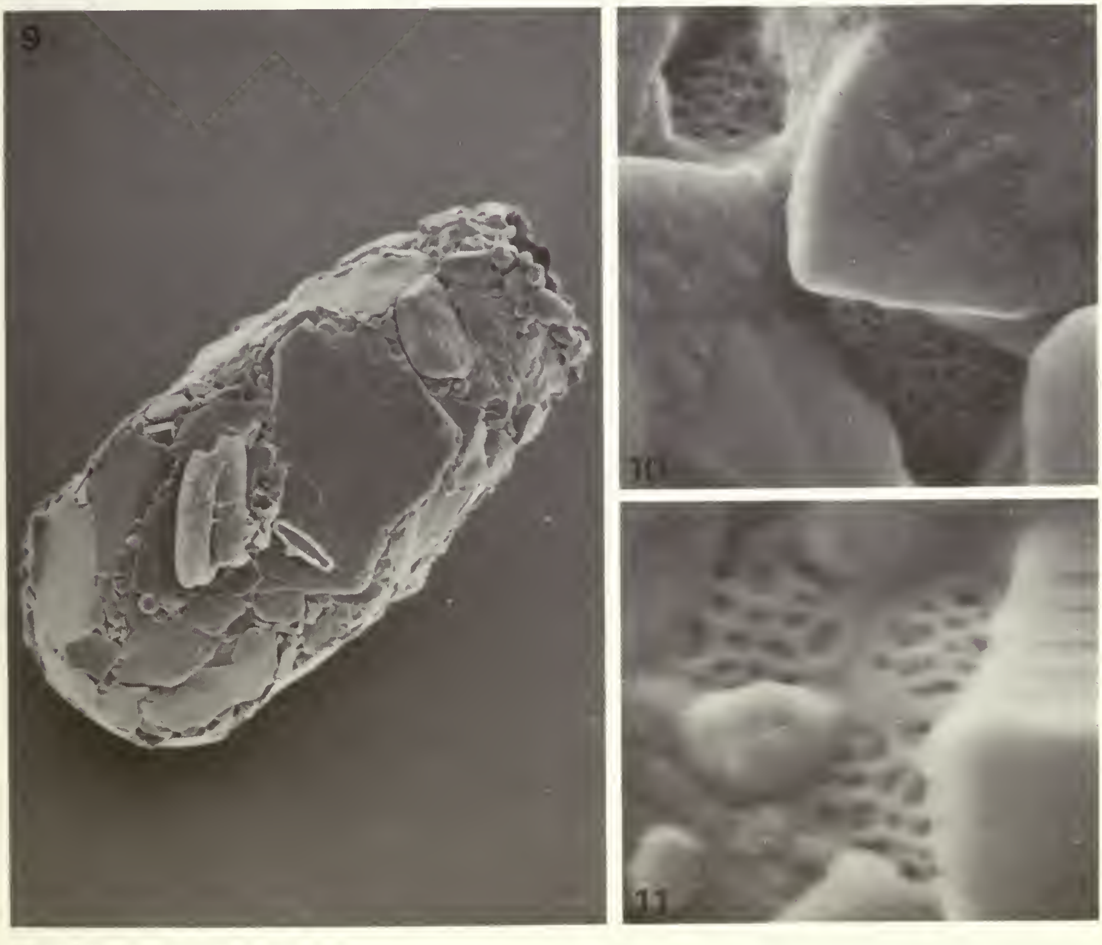
Figs 3–6 *Cyphoderia laevis:* Fig. 3, lateral view of aperture ×3000; Fig. 4, view of shell to show curvature of outline ×1700; Fig. 5, apertural view ×1300; Fig. 6, detail of shell surface ×10000.

Difflugia amophoralis Cash & Hopkinson, 1909

Two species examined: body length 108 & 110 μm, breadth 67 & 70 μm, diameter of aperture 32 & 37 μm, similar to Fig. 19, Ogden, 1983*b*. These specimens agree well with the earlier description (Ogden, 1983*b*) being composed mainly of quartz, but they also incorporate some spherical siliceous flagellate cysts.



Figs 7 & 8 *Difflugia acuminata:* Detail of organic cement pattern ×34000 and ×39000.



Figs 9–11 *Difflugia bryophila:* Fig. 9, lateral view to illustrate basic outline ×960; Figs 10 & 11, detail of organic cement network × 27000 and × 49000.

Difflugia bicornis Penard, 1890

Fifteen specimens examined: body length 63–91 µm, breadth 36–51 µm, diameter of aperture 18–25 µm, similar to Fig. 2, Ogden & Živković, 1983, but all of these specimens have only one aboral spine.

Difflugia brevicolla Cash & Hopkinson, 1909

Eight specimens examined: body length 84–119 µm, breadth 79–100 µm, diameter of aperture 36–46 µm, similar to Figs 13–17, Ogden, 1980.

Difflugia bryophila (Penard, 1902)

Five specimens examined: body length 99–136 µm, diameter of aperture 17–22 µm. The specimens are typical of those already described (compare Fig. 9 with Fig. 1, Ogden, 1983*b*), but the organic cement is now seen at higher magnification to be a network with a distinct pattern (Figs 10 & 11).

Difflugia capreolata Penard, 1902

One specimen examined: body length 237 µm, breadth 164 µm, diameter of aperture 65 µm, this specimen is similar to Fig. 3, Ogden & Živković, 1983.

Difflugia distenda Ogden, 1983

Three specimens examined; body length 199–222 µm, breadth 91–108 µm, diameter of aperture 47–54 µm, similar to Fig. 21, Ogden, 1983*b*.

Difflugia elegans Penard, 1890

Six specimens examined: body length 95–129 µm, breadth 55–66 µm, diameter of aperture 30–36 µm, similar to Plate 55, Ogden & Hedley, 1980 and Figs 5 & 11, Ogden, 1979*a*.

Difflugia elegans var. ***angustata*** Gauthier-Lièvre & Thomas, 1958

DESCRIPTION. The shell is usually transparent, elongate with an aboral horn, composed of angular quartz and an occasional diatom frustule (Fig. 12). An organic cement network (Fig. 14) similar to that seen in *D. elegans* (Fig. 15) is present (see Ogden, 1979*a*). The only feature that differentiates these specimens from *D. elegans* is the elongate shape of the body and the absence of a constriction near the aperture (Figs 12 & 13).

MEASUREMENTS (in µm). Based on four specimens: body length 95–118, breadth 44–51, diameter of aperture, 24–27.

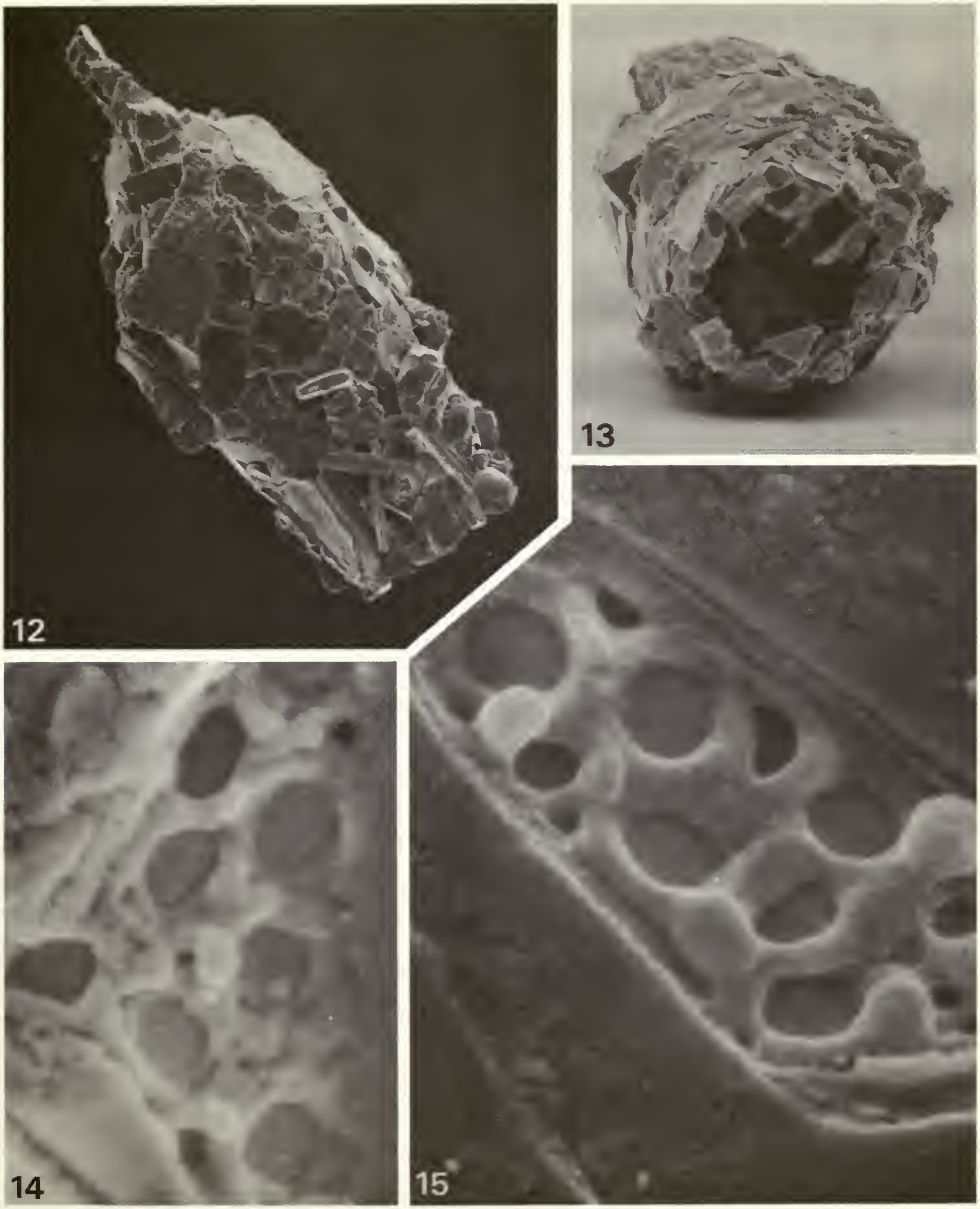
REMARKS. Although the slimness of the body and the smaller aperture give reduced ratios for both, breadth/body length (0·44) and diameter of aperture/body length (0·24) when compared with the type species (0·59 ± 0·07; 0·33 ± 0·04, see Ogden, 1979*a*) there are too few specimens on which to base an accurate assessment of the specificity of this variety, and it is therefore described as such.

Difflugia lanceolata Penard, 1890

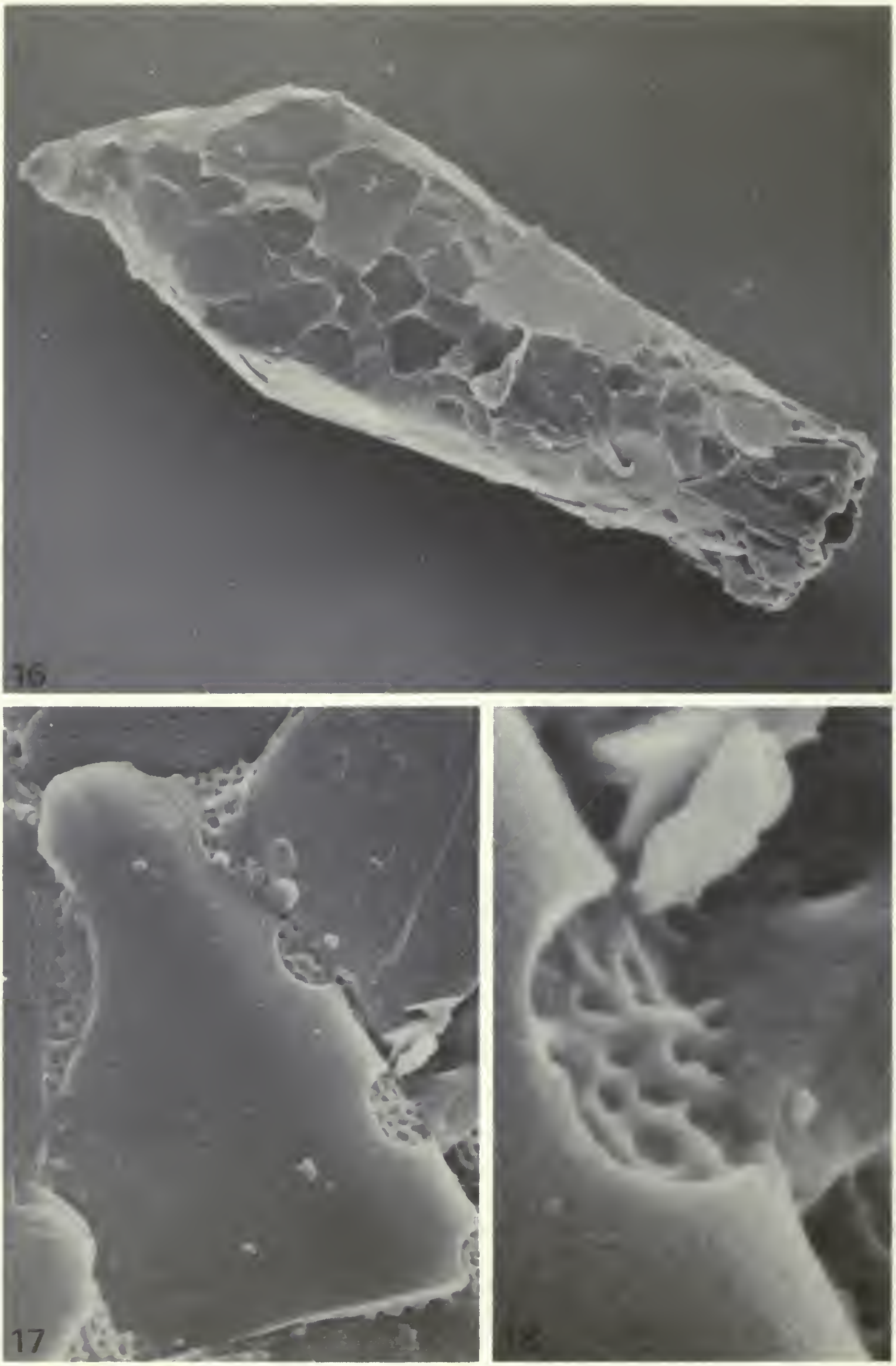
Three specimens examined: body length 162–173 µm, breadth 60–67 µm, diameter of aperture 24–32 µm, similar to Fig. 6, Ogden, 1983*b*.

Difflugia lismorensis Playfair, 1918

Two species examined: body length 144 & 151 µm, breadth 96 & 89 µm, diameter of aperture 37 & 39 µm, similar to Fig. 8, Ogden & Živković, 1983.



Figs 12–14 *Difflugia elegans* var. *angustata:* Fig. 12, lateral view, note the almost parallel sides ×840; Fig. 13, apertural view ×900; Fig. 14, detail of organic cement ×34000; **Fig. 15,** *Difflugia elegans,* detail of organic cement ×34000.



Figs 16–18 *Difflugia oranensis:* Fig. 16, lateral view showing the aboral projection ×1500; Fig. 17, portion of surface to illustrate the distribution of organic cement ×12000; Fig. 18, detail of organic cement ×45000.

Difflugia lucida Penard, 1890

Two specimens examined: body length 61 & 69 µm, breadth 38 & 44 µm, depth 29 µm, diameter of aperture 22 & 25 µm, similar to Fig. 43, Ogden, 1983*b*.

Difflugia manicata Penard, 1902

Two species examined: body length 55 µm, breadth 46 & 47 µm, diameter of aperture 19 & 20 µm, similar to Fig. 50, Ogden, 1983*b* and Fig. 9, Ogden & Živković, 1983.

Difflugia oranensis Gauthier-Lièvre & Thomas, 1958

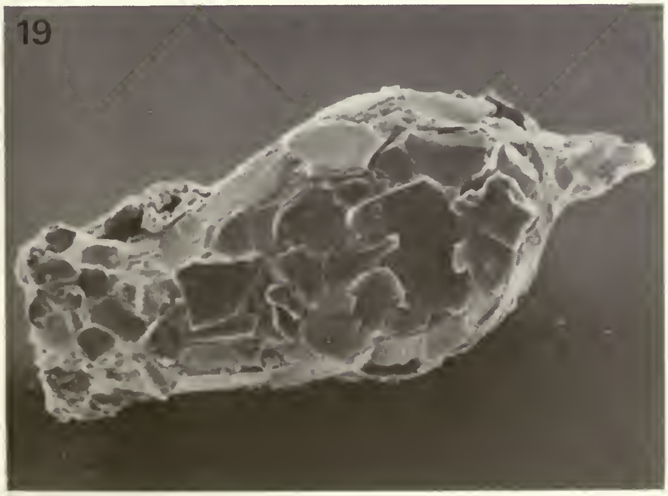
Difflugia mamillaris var. *oranensis* Gauthier-Lièvre & Thomas, 1958

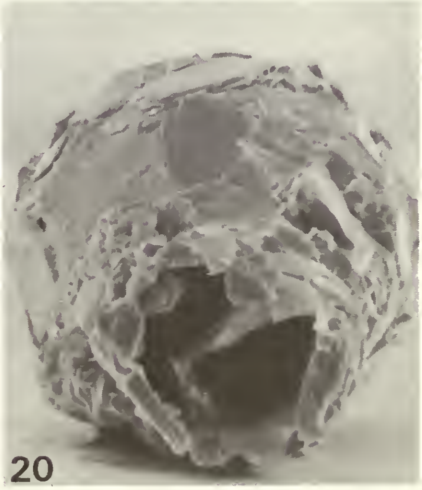
DESCRIPTION. The shell is transparent, slim, elongate, slightly widened at the aperture tapering to the mid-body point and then swelling slightly until it tapers gently to a small aboral projection (Fig. 16). It is composed mainly of flattened pieces of quartz, with an occasionl piece of flattened diatom frustule, arranged to give, in general, a smooth regular outline. The particles are bound together by organic cement, which has a typical network pattern with walls 0·12 µm thick and a mesh with a diameter of about 0·10 µm (Figs 17 & 18). The aperture is circular and usually surrounded by small particles.

MEASUREMENTS (in µm). Based on six specimens: body length 79–93, breadth 20–32, diameter of aperture 13–15.

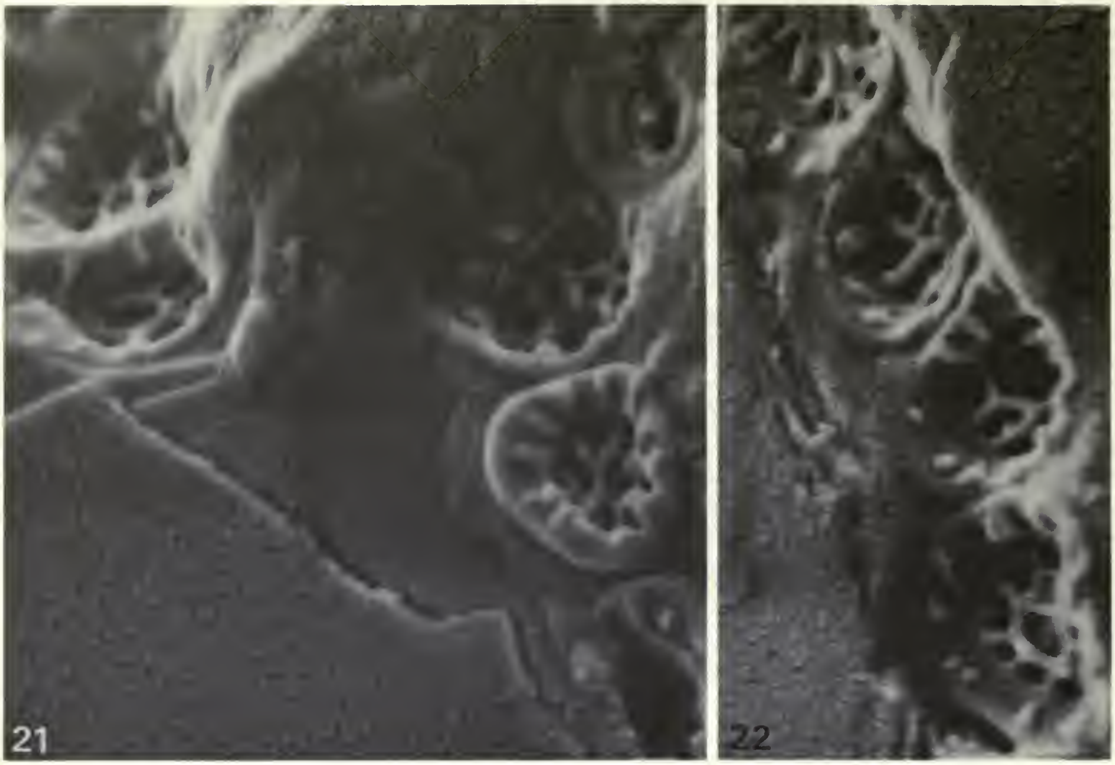
REMARKS. In describing the variety *oranensis* Gauthier-Lièvre & Thomas (1958) stated that it was compressed and had an elongate aperture, those described here although agreeing well in all other respects, disagree on these two points. However, the present specimens are considered to be fragile and liable to collapse or distort if handled roughly, sufficient for them to agree with the original description. For this reason it is considered that they be treated as being identical with *D. oranensis*.

Three smaller specimens, measuring 61–73 µm in length, 31–35 µm in breadth and having apertures 13–15 µm in diameter, of a similar shape are also tentatively assigned to *D. oranensis*. These specimens differ not only in length but have a more pronounced swelling in the aboral region (Figs 19 & 20). They share a similar organic cement pattern with the specimens of *D. oranensis* described above. It may well be that they represent a distinct species but there are insufficient specimens to make adequate comparisons.





Figs 19–20 *Difflugia oranensis* (?): Fig. 19, view to show the more swollen mid-body region (compare with Fig. 16) ×1100; Fig. 20, apertural view ×1600.



Figs 21 & 22 *Difflugia parva:* Detail of organic cement units ×37000.

Difflugia parva (Thomas, 1954)

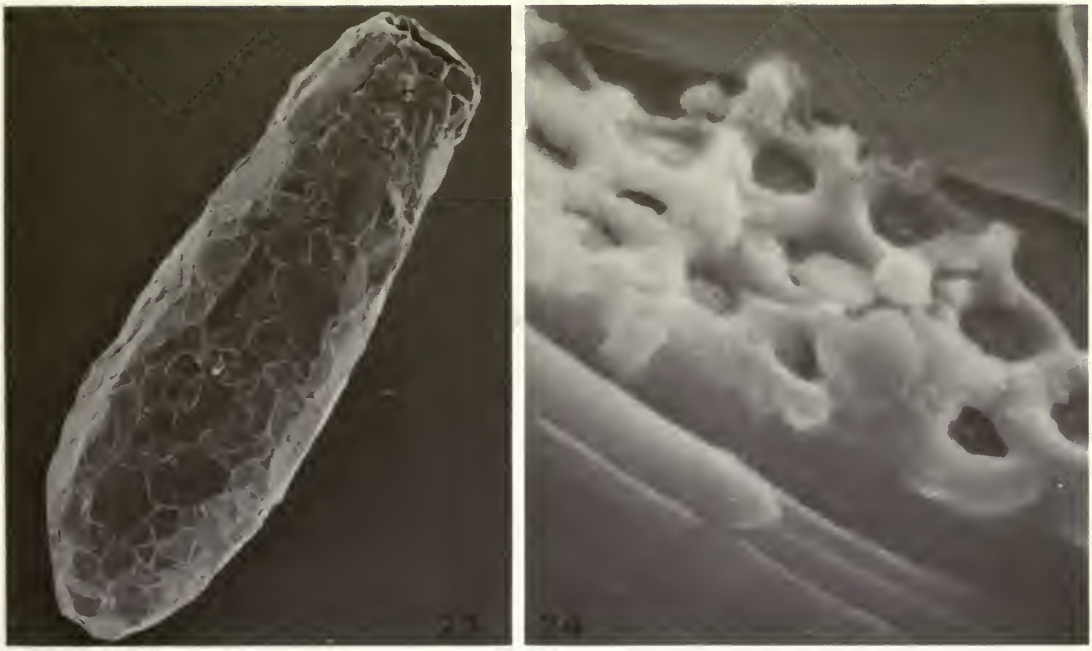
Five specimens examined: body length 168–224 µm, breadth 77–103 µm, diameter of aperture 24–40 µm, these specimens agree with the description already given by Ogden (1983*b*). The detail of the small mesh, covering the inner portion of each network enclosure, is now clearly seen in Figs 21 & 22.

Difflugia paulii Ogden, 1983

Five specimens examined: body length 85–130 µm, breadth 28–46 µm, diameter of aperture 14–22 µm, these specimens have the typical cigar-shape (Fig. 23) and smooth shell, the cement is seen here as a network (Fig. 24). They agree well with the original description (Ogden, 1983*b*).

Difflugia pecac sp. nov.

DESCRIPTION. The shell is transparent, elongate almost cylindrical except that the widest diameter is in the latter third of the body length (Fig. 25), the aboral extremity may be either smoothly rounded or occasionally pointed (Fig. 27). It is often slightly compressed in the first third of the body length, but some specimens show no compression at all, and the aperture is therefore either elongate or oval in outline (Fig. 26). The structure is composed mainly of thin flattish pieces of quartz, flattish diatom particles are frequently included, arranged to make a smooth surface with small particles surrounding the apertural opening. Organic cement binds these particles and is usually restricted to small areas between these neatly arranged pieces, but may sometimes be seen as a network. In small areas it appears as an arrangement of rings (Fig. 28), but in a larger area it is seen as a typical network of walls and depressions (Figs 29 & 30).



Figs 23 & 24 *Difflugia paulii:* Fig. 23, lateral view to illustrate typical cigar-shape ×700; Fig. 24, detail of organic cement network ×27000.

Measurements (in µm). Based on twenty-two specimens: body length 62–84, breadth 25–36, depth 19–30, diameter of aperture 12–22.

Remarks. The fragility of this species may account for the variable degree of compression seen in the anterior third of the body. The other alternative is that these specimens may be comprised of two closely similar forms, one slightly compressed and the other having a more rounded aboral extremity. Nevertheless, as a whole they appear to represent a previously undescribed species. The compressed nature of *D. pecac* makes it most similar to *D. lucida.* It differs in body shape, having a regular slim outline with almost parallel sides and a smoothly rounded aboral extremity, whereas *D. lucida* is characteristically oval in outline and has a curved extremity (see Ogden, 1983*b*).

Etymology. This species is named after the unknown fisherman, pècāč = fisherman (Serbo-croatian), who kindly ferried us across Lake Vlasina in his boat and assisted us in our landing on the floating mass of vegetation.

Difflugia petricola Cash, 1909

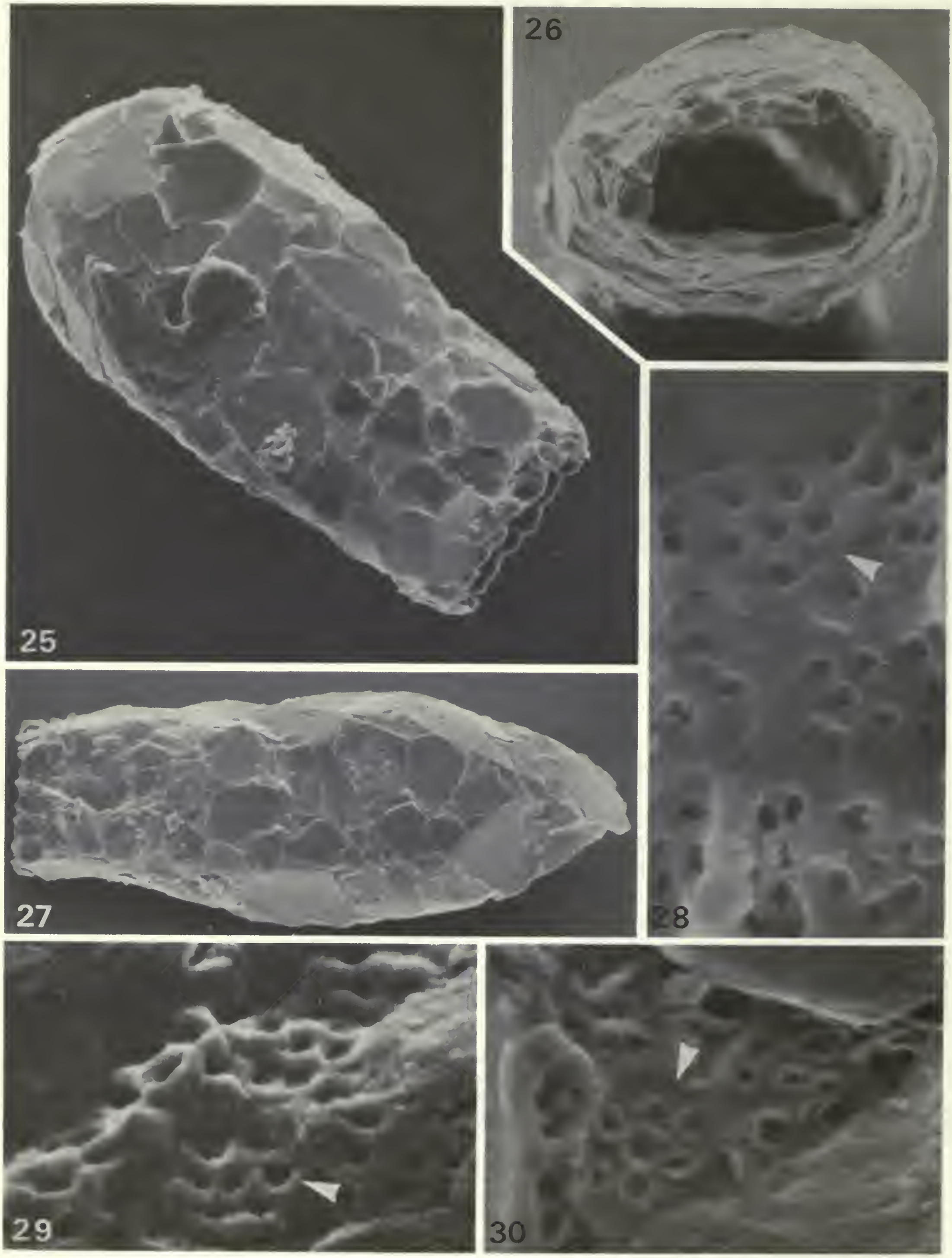
Sixteen specimens examined: body length 80–105 µm, breadth 58–74 µm, diameter of aperture 21–29 µm, similar to Figs 4–6, Ogden & Fairman, 1979.

Difflugia pristis Penard, 1902

Eighteen specimens examined: body length 41–50 µm, breadth 22–39 µm, diameter of aperture 9–16 µm, similar to Fig. 12, Ogden, 1983*b*.

Difflugia pulex Penard, 1902

Five specimens examined: body length 33–39 µm, breadth 22–31 µm, diameter of aperture 10–14 µm, similar to Fig. 14, Ogden, 1983*b*.

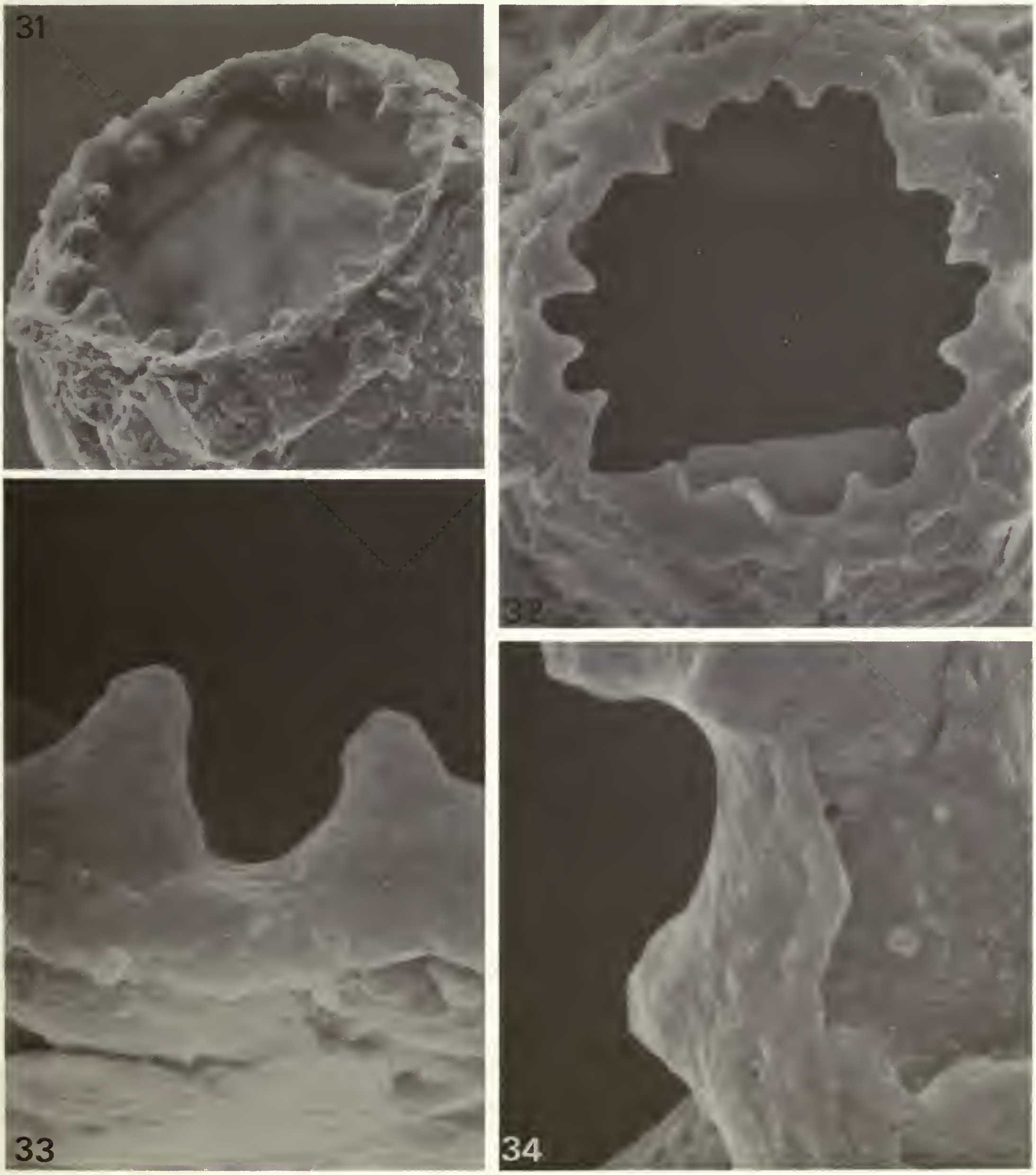


Figs 25–30 *Difflugia pecac* sp. nov.: Fig. 25, lateral view to show the almost parallel sides × 1500; Fig. 26, apertural view × 1800; Fig. 27, view to illustrate the pointed aboral extremity and lateral compression × 1300; Figs 28–30, detail of organic cement network, each unit (arrowed) appears to be composed of a central ring surrounded by five or six similar rings × 35000, × 35000 & × 30000.

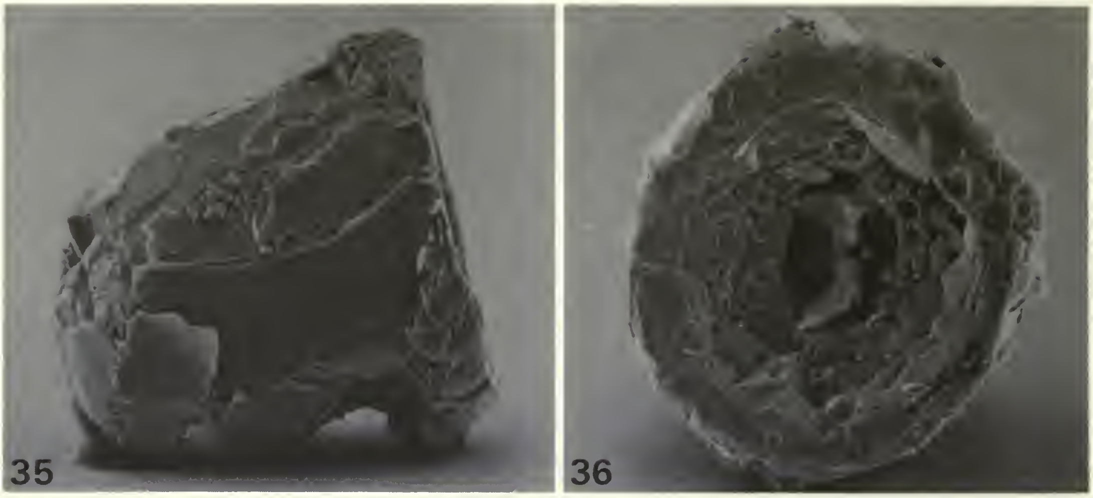
Difflugia rubescens Penard, 1891

Three specimens examined: body length 57–80 µm, breadth 41–44 µm, diameter of aperture 15–20 µm, similar to Plate 66, Ogden & Hedley, 1980.

Detail of the organic tooth-like structures surrounding the aperture (Figs 31 & 32) are included here to show that this character is a distinct rim of smooth cement. The 'teeth' are irregular in distribution but can often be precise in construction (Fig. 33), and the cement is limited to a narrow band (Figs 32 & 34).



Figs 31–34 *Difflugia rubescens:* Fig. 31, latero-apertural view showing the ring of 'tooth-like' structures ×2800; Fig. 32, apertural view to show uneven distribution of 'teeth' ×3800; Figs 33 & 34, detail of featureless organic cement rim and 'teeth' ×14000 & ×17000.



Figs 35 & 36 (?) *Difflugia:* Fig. 35, lateral view ×700; Fig. 36, apertural view, note the invaginated aperture ×800.

Difflugia ventricosa Deflandre, 1926

Two specimens examined: body length 221 & 237 µm, breadth 191 & 219 µm, diameter of aperture 85 & 114 µm, similar to Fig. 39, Ogden, 1983*b*.

(?) *Difflugia* sp.

A single specimen 78 µm long, 66 µm breadth and diameter of aperture 23 µm, was found which appears to represent a previously unknown species. The shell construction (Fig. 35) is typical of a *Difflugia*-type shell, but the invaginated aperture (Fig. 36) is more typical of the *Centropyxis*-type shell. It is here considered as a possible species of *Difflugia*.

Euglypha acanthophora (Ehrenberg, 1841)

Four specimens examined: shell length 75–85 µm, breadth 38–41 µm, diameter of aperture 19–22 µm, similar to Figs 1–5, Ogden, 1981.

Euglypha cristata Leidy, 1874

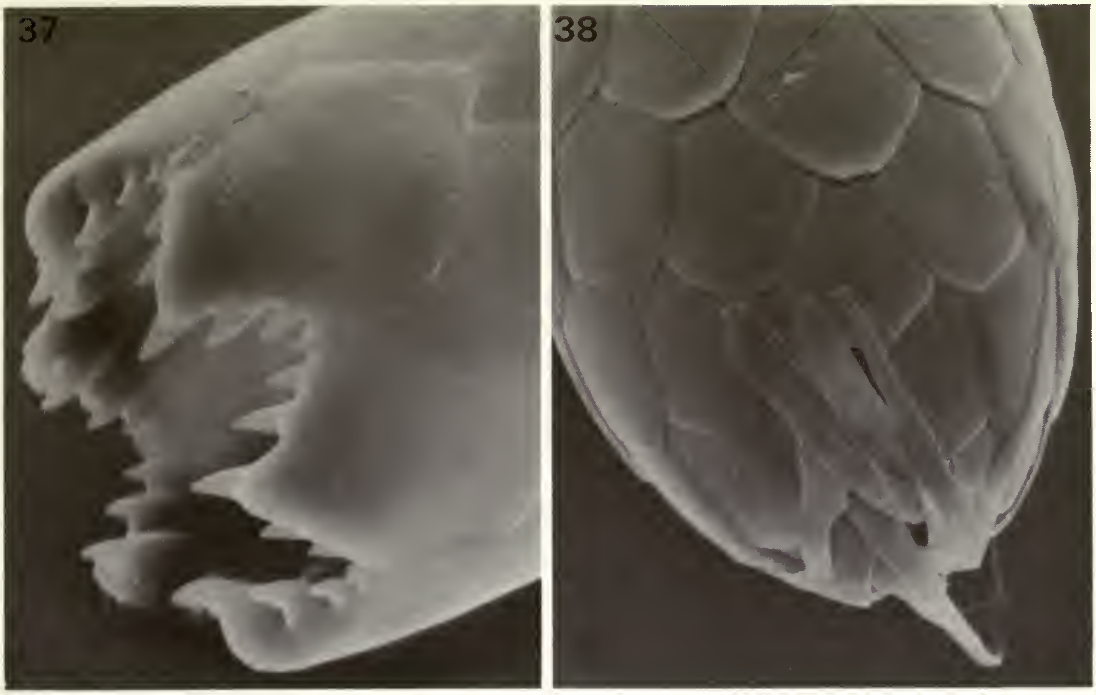
One specimen examined: shell length 54 µm, breadth 15 µm, diameter of aperture 8 µm, similar to Plate 79, Ogden & Hedley, 1980. There are six apertural plates on this specimen, each being thickened at the denticular margin (Fig. 37) and having a small protrusion at the opposite margin. As noted earlier (Ogden & Hedley, 1980) the spines that protrude from the aboral extremity appear to be flexible, in this instance the flattened structures are curved back over the body surface (Fig. 38).

Euglypha rotunda Wailes, 1911

Three specimens examined: shell length 37–40 µm, breadth 21–32 µm, depth 15–16 µm, diameter of aperture 8–9 µm, similar to Plate 82, Ogden & Hedley, 1980.

Euglypha tuberculata Dujardin, 1841

Six specimens examined: shell length 64–82 µm, breadth 28–47 µm, diameter of aperture 13–20 µm, similar to Plate 84, Ogden & Hedley, 1980. A clonal culture of this species was



Figs 37 & 38 *Euglypha cristata:* Fig. 37, latero-apertural view to illustrate detail of apertural plates ×8000; Fig. 38, aboral region showing the spines folded onto the shell surface ×5000.

maintained in the Museum for several months. Specimens from this culture were identical to those found from the wild, although in culture several specimens having a double complement of shell and apertural plates were observed. This phenomenon of larger individuals has already been reported from other cultures of siliceous testate amoebae (Hedley & Ogden, 1973).

Heleopera petricola Leidy, 1879

Seven specimens were examined: shell length 95–102 µm, breadth 52–78 µm, depth 35–44 µm, diameter of aperture 29–44 µm, similar to Plate 27, Ogden & Hedley, 1980.

Hyalosphenia papilio Leidy, 1875

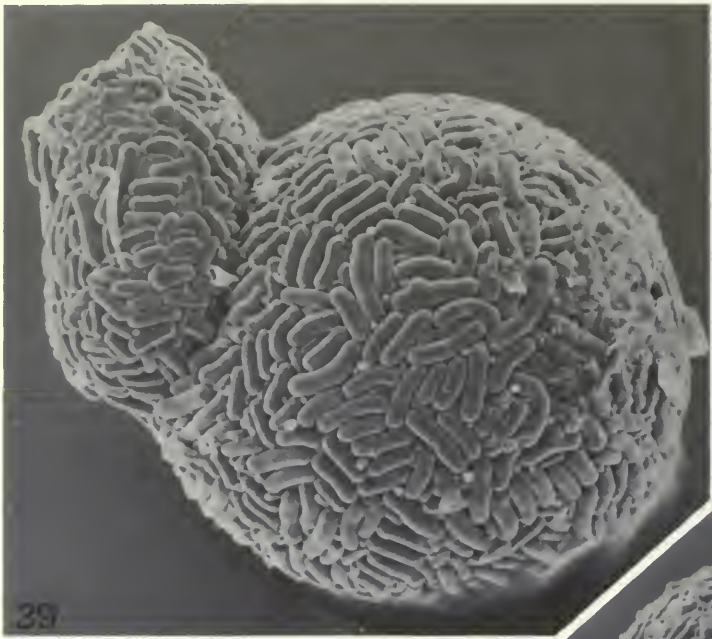
Two specimens examined: shell length 112 & 118 µm, breadth 67 & 70 µm, depth 26 µm, diameter of aperture 30 & 32 µm, similar to Plate 25, Ogden & Hedley, 1980.

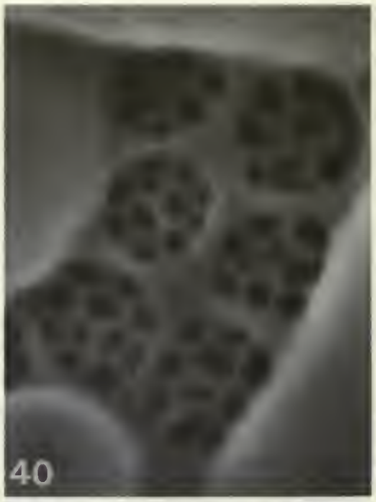
Lesquereusia epistomum Penard, 1902

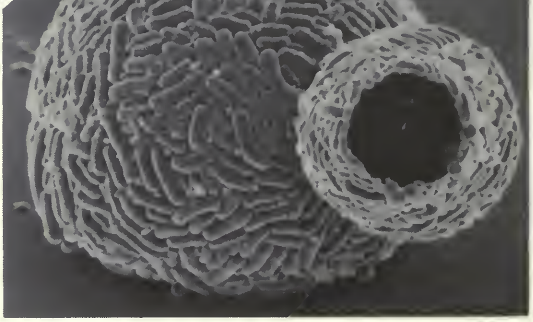
Two specimens examined: shell length 116 & 127 µm, breadth 67 & 75 µm, diameter of aperture 20 & 33 µm. Although only two specimens were examined this was one of the most abundant species present in the samples, being easily distinguished by the distinct neck and ovoid shape (Figs 39 & 41). The typical cement network (Fig. 40) is the same as that described for *L. spiralis* by Ogden (1979*b*).

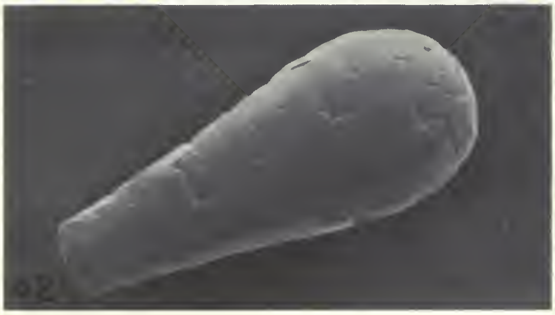
Lesquereusia spiralis (Ehrenberg, 1840)

Four specimens examined: shell length 94–108 µm, breadth 75–97 µm, diameter of aperture 20–32 µm, similar to Plate 32, Ogden & Hedley, 1980.









Figs 39–41 *Lesquereusia epistomium:* Fig. 39, lateral view, note the distinct neck ×700; Fig. 40, detail of organic cement ×25000; Fig 41, apertural view ×700. **Fig. 42,** *Quadrulella symmetrica:* lateral view of elongate specimen ×500.

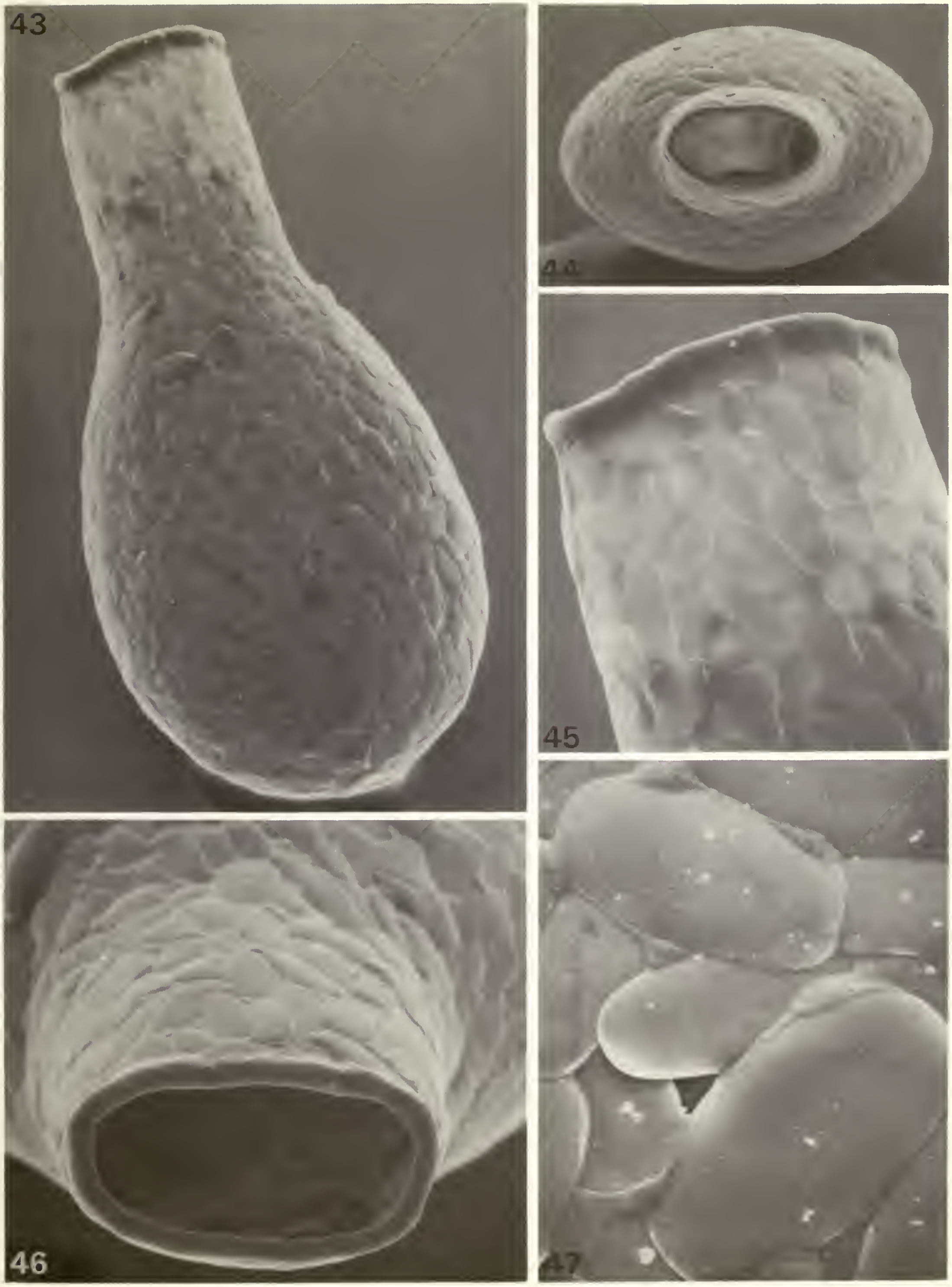
Nebela dentistoma Penard, 1890

Two specimens examined: shell length 104 & 108 µm, breadth 67 & 77 µm, depth 51 & 56 µm, diameter of aperture 21 & 23 µm, similar to Plate 37, Ogden & Hedley, 1980.

Nebela lageniformis Penard, 1890

DESCRIPTION. The shell is transparent, colourless or slightly yellow, ovoid with a distinct neck (Fig. 43) and laterally compressed (Fig. 44). It is composed of a mixture of circular, oval or elongate shell plates, the illustrated specimen is atypical being composed of mainly elongate plates. These plates are usually distributed at random and may overlap each other, a featureless cement binds them together (Fig. 47). The aperture has a small lip (Fig. 45) which is surrounded by a small rim of organic cement (Fig. 46). It is oval or like an elongated slit (Fig. 46).

MEASUREMENTS (in µm). Based on five specimens: shell length 98–120, breadth 50–69, depth 39–43, diameter of aperture 9–12 × 19–25.



Figs 43–47 *Nebela lageniformis:* Fig. 43, view to show the general outline with distinct neck ×1200; Fig. 44, apertural view ×900; Fig. 45, detail of neck and apertural collar ×2500; Fig. 46, view showing apertural opening and surrounding organic collar ×2500; Fig. 47, detail of shell surface ×800.

REMARKS. The specimens described here are in good agreement with both of Penard's earlier descriptions (1890 & 1902).

Nebela penardiana Deflandre, 1936

Six specimens examined: shell length 99–169 µm, breadth 50–86 µm, depth 27–62 µm, diameter of aperture 17–32 µm, similar to Plate 42, Ogden & Hedley, 1980.

Nebela vitrae Penard, 1899

One specimen examined: shell length 126 µm, breadth 80 µm, depth 45 µm, diameter of aperture 26 µm, similar to Plate 46, Ogden & Hedley, 1980.

Netzelia tuberculata (Wallich, 1864) Netzel, 1983

Five specimens examined: shell length 105–139 µm, breadth 86–120µm, diameter of aperture 28–40 µm, similar to Plate 67, Ogden & Hedley, 1980. This species originally described as *Difflugia tuberculata,* was mentioned by Ogden (1979*b*) as being a possible candidate for the genus *Netzelia* Ogden, 1979 because of the earlier ultrastructural studies of Eckert & McGee-Russell (1974) and Owen & Jones (1976). More recent studies by Netzel (1983) and Meisterfeld (as reported at the IIIrd International Workshop on Testate Amoebae in Aachen, 1983) have shown that this species produces its own siliceous idiosomes plus the organic building material that binds these idiosomes together, and they therefore propose its transfer to the genus *Netzelia.*

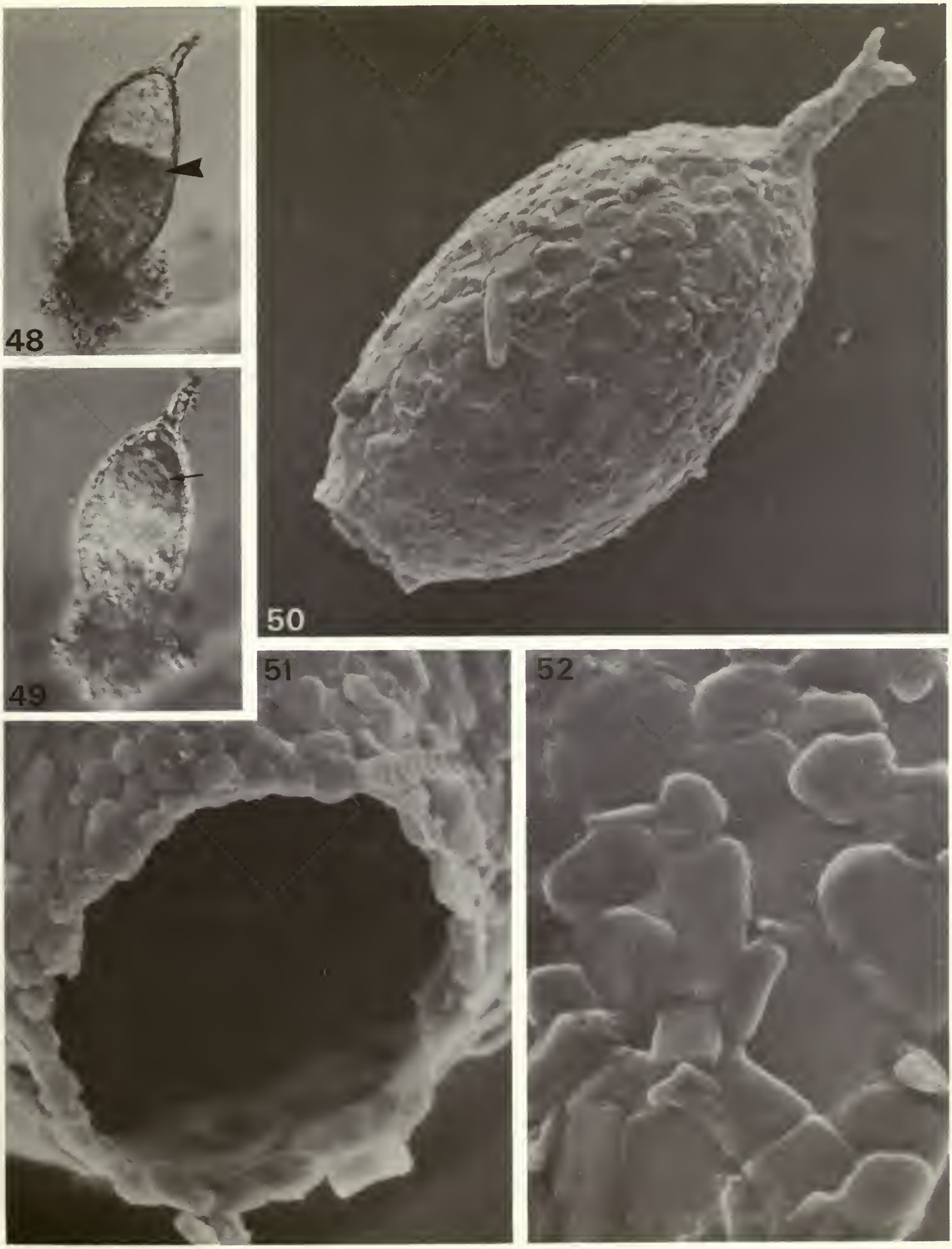
Paraeuglypha reticulata, Penard, 1902

Difflugia delicatula Gauthier-Lièvre & Thomas, 1958

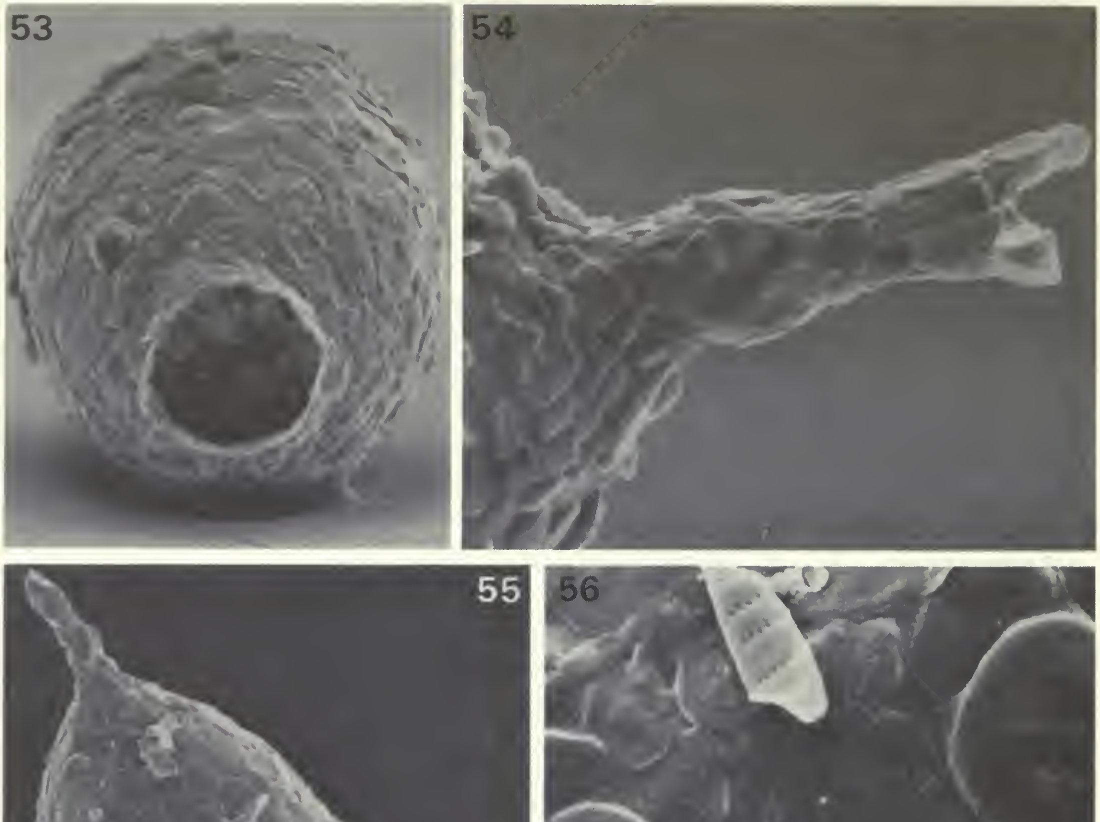
DESCRIPTION. A few live animals were observed, which had a large central nucleus in the posterior half of the cytoplasm, and a band of dense particles positioned in front of this across the mid-body region (Fig. 48). The latter feature is identical to the pigment zone seen in species of the family Euglyphidae. No pseudopodia were observed as the aperture was surrounded by an assemblage of particulate material (Fig. 49). The shell is transparent and pale yellow in colour, elongate ovoid in shape tapering at the aperture to a small collar and aborally to a thin slightly tapered central spine or projection (Fig. 50). The projection is built as an extension of the shell and varies in both length and shape, specimens with single and bifurcate points have been seen (Fig. 54). A mixture of small and medium-sized, oval, circular and elongate shell plates, cover the shell surface (Fig. 52). An occasional diatom frustule has also been seen in this assemblage. Organic cement binds these particles together and is seen as a smooth sheet between some junctions. The aperture is round and usually surrounded by a small raised collar (Figs 51 & 53).

MEASUREMENTS (in µm). Based on 14 specimens: body length 79–98, breadth 34–44, diameter of aperture 12–19.

REMARKS. *Paraeuglypha* was erected by Penard (1902) to accommodate a new species *P. reticulata,* an unusual animal which had shell plates similar to those described for *Euglypha,* but a thin aboral spine. The shell was yellow, elongate, pyriform or fusiform and not compressed, the shell plates were round or oval but often with irregular outlines. There was a zone of 'grains brillants', now referred to as the pigment zone, just anterior to the nucleus. Filiform pseudopodia were observed, but most frequently the aperture was surrounded by an assemblage of extraneous material. Penard considered it to be a rare species as he only found it in three samples. The present description agrees well within the animals described by Penard, there was a pigment zone in live animals and the shells are similar in colour, size and shape.



Figs 48–52 *Paraeuglypha reticulata:* Fig. 48, optical micrograph of living animal to show the dark pigment zone (arrowed) ×500; Fig. 49, optical micrograph illustrating the nucleus (arrowed), extraneous material surrounds the aperture ×500; Fig. 50, lateral view, note the small apertural collar and distinct aboral protuberance ×1300; Fig. 51, detail of apertural collar ×4500; Fig. 52, detail of shell surface ×6000.



Figs 53–56 *Paraeuglypha reticulata:* Fig. 53 apertural view ×1300; Fig. 54, detail of aboral protuberance, note the mixture of different shell plates ×3700; Fig. 55, specimen with shell composed almost entirely of circular shell plates ×1600; Fig. 56, detail of shell surface ×7500.

A new species of *Difflugia, D. delicatula* was described by Gauthier-Lièvre and Thomas (1958) as having an ovoid or ellipsoid shell with a long anterior spine. It was covered with small polygonal particles and one specimen had used small circular plates from the diatom *Echinornic crassipes.* Again it was considered to be a rare species. It would appear that this description was based on observations of shells alone, as observations of living animals were not recorded. It is also in good agreement with the present specimens, being composed of a mixture of different sized small particles, and is here considered to be a synonym of *P. reticulata.*

The most interesting feature of the present specimens is the presence of a pigment zone, which imply that the animal has a facility for producing its own shell plates. Nevertheless, it does not appear to produce a shell constructed only of shell plates arranged in a regular, evenly spaced shell as seen in specimens belonging to the family Euglyphidae, but instead has an apparent mixture of shell plates and extraneous material. This assemblage of particles in some instances resembles a mixture more frequently seen in species of *Nebela,* but here the resemblance ends because of their irregular arrangement. The arrangement is most similar to that seen in small fragile specimens belonging to the family Difflugiidae, but members of these two groups have lobose pseudopodia. In summary, it would appear that this species represents a link between those animals that have lobose pseudopodia, produce their own shell components and can also incorporate extraneous particles, for example *Netzelia* and *Lesquereusia* (see Ogden, 1979*b*), with those which have filiform pseudopodia and a shell composed of arranged shell plates.

Plagiopyxis penardi Thomas, 1955

One specimen examined: shell length 88 µm, breadth 43 µm, diameter of aperture 34 µm, similar to Figs 7–11, Ogden, 1984.

Pseudodifflugia gracilis Schlumberger, 1845

Two specimens examined: shell length 63 & 72 µm, breadth 42 & 48 µm, diameter of aperture 41 & 36 µm, similar to Plate 76, Ogden & Hedley, 1980.

Quadrulella symmetrica (Wallich, 1863)

Four specimens examined: shell length 88–135 µm, breadth 49–62 µm, depth 33–37 µm, diameter of aperture 19–24 µm, similar to Plate 47, Ogden & Hedley, 1980. Three of these specimens were more elongate (Fig. 42) than the typical specimen shown in Plate 47 (Ogden & Hedley, 1980), and such specimens have been described as *Q. symmetrica* var. *longicollis* by Chardez (1964). However, these shells could represent the extra large specimens often seen in species of *Euglypha,* for example *E. tuberculata* as described on p. 254 above, and for that reason are not differentiated from the typical *Q. symmetrica.*

Sphenoderia lenta Schlumberger, 1845

Two species examined: shell length 45 & 50 µm, breadth 38 & 34 µm, diameter of aperture 16 & 14 µm, similar to Plate 89, Ogden & Hedley, 1980, and Figs 50–54, Ogden, 1984.

Sphenoderia sp.

Two specimens exmined: shell length 40 & 45µm, breadth 28 & 27 µm, diameter of aperture 14 µm, similar to those specimens described by Ogden (1984, Figs 45–49) having fewer shell plates than the typical *S. lenta.*

Trinema enchelys (Ehrenberg, 1838)

Six specimens examined: shell length 39–60 µm, breadth 22–29 µm, depth 18–27 µm, diameter of aperture 10–13 µm, similar to Plate 91, Ogden & Hedley, 1980.

Discussion

The agreement found between the organic cement patterns of species of *Difflugia* collected in Britain and Yugoslavia establishes this feature as a good taxonomic character. These organic elements are produced by the animal as individual units, they are used as such or combined assemblages to bind the shell components together. The difference in the structure of these elements is probably related to the type of construction built by a particular species, and there appears to be some correlation between the cement used by species which construct similar shells. This similarity does not necessarily relate to shape, although some are similar, but more especially to the type of material used and the way it is blended together in construction. For example, *Difflugia parva* and *D. cylindrus* have similar organic cement patterns and construct elongate, cylindrical shells having a rough surface using a mixture of angular quartz particles, whilst *D. mamillaris* and *D. ampululla* have another type of organic cement but construct different shaped smooth shells using mainly flattish quartz particles. Recent ultrastructural studies (Netzel, 1983) on shell formation in *Netzelia oviformis* have shown that these organic elements are prefabricated in the Golgi apparatus and transported through the cytoplasm to the plasmalemma. They are extruded and placed by finger-like processes between adjacent inorganic idiosomes, to which they become attached and form the shell casing. This behaviour is similar to the positioning of siliceous plates in shell formation by species of *Eugylpha* as described by Hedley & Ogden (1974) and Ogden (1979*c*).

The finding of *Paraeuglypha* in the present samples appears to suggest another type of shell formation in the Class Filosea. To date all members of the family Euglyphidae are considered to produce shell plates of uniform outline. These may be circular, oval or elongate, within a range of different sizes, a mixture of which may be incorporated in one shell, and some species additionally produce spines. Such siliceous shell plates are usually organized into distinct patterns, or regular arrangements, and no extraneous material is incorporated into the shell. *Paraeuglypha* comes close to the definition but is differentiated by producing irregular shaped shell plates and it also appears to incorporate some extraneous material.

Acknowledgements

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Description of a neotype for the holothurian *Ocnus brunneus* (Forbes MS *in* Thompson, 1840) from Strangford Lough, Northern Ireland (Holothurioidea; Dendrochirotida)

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Introduction

Ocnus brunneus was first described in a brief footnote on p. 100 of a paper by Thompson on molluscs and other invertebrates of Ireland as follows:

> *Holothuria brunnea* Forbes MS
> Holothuria brown, angulated, suckers 6 to 8 in each row, tentacula long whitish, pinnated towards their extremities. Forbes.
> This minute Holothuria, generally under an inch in length, is the most common species taken by dredging in the loughs of Strangford and Belfast.

However, Forbes himself in 1841 (p. 230) recorded the species from the Firth of Clyde and the Isle of Man when he gave a fuller description, referring it to the new genus *Ocnus* (cited as 'Forbes & Goodsir') together with *Holothuria lactea* Forbes & Goodsir, 1839. The name *Ocnus* was subsequently either synonymized with *Cucumaria* or inadmissably used for species other than the two named above until Panning (1949) revived it, designating *brunneus* Forbes as type species. However, no type material is known to exist and considerable confusion has arisen over the identity of this little holothurian. Hérouard (1889) considered *brunneus* to be a valid species of *Cucumaria* but Mortensen (1927) could find no differences, except in colour, between it and *lacteus* and regarded them as synonymous. Despite this, albeit with reservations, he accepted *Cucumaria brunnea*: sensu Koehler, 1921, as a valid species though not conspecific with *O. brunneus* (Forbes). Mortensen's opinion has led to specimens agreeing with the description of *brunneus* being described and figured under the name of *Cucumaria lactea* in several popular shore guides (Eales, 1952; Barrett & Yonge, 1958; Barnes, 1979).

However, Cherbonnier (1951) examining (presumably) small brown specimens from Roscoff, Brittany, including three named *brunnea* by Hérouard, concluded that these are conspecific with young *C. planci* (Brandt, 1835) from Mediterranean and Belgian localities. He therefore synonymized *brunneus* with *planci,* which he retained in *Cucumaria.* Panning (1971: 33–34) maintained *Ocnus* as a genus distinct from *Cucumaria* and discussed the problem at some length, suggesting initially that three species together extend between Senegal and mid-Norway: *O. planci* ranging from Senegal to the west of England, *O. lacteus* from the east of England to Scandinavia, and *O. brunneus* in southern England and northern France (without mention of Northern Ireland). However, he finally agreed with Cherbonnier that *brunneus* represents young *planci* and the latter name, being older, should be accepted for the type species of *Ocnus.* Rowe (1970) adopted Mortensen's synonymy of *brunneus* with *lacteus* but accepted the genus *Ocnus.*

In view of the controversy about the validity and identity of *O. brunneus* and its status as the nominal type species of *Ocnus* Forbes and Goodsir *in* Forbes, 1841, the establishment of a neotype for *brunneus* in the absence of original Forbes or Thompson material is highly desirable. Specimens matching the description and figure of *brunneus* (Forbes, 1841) have

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frequently been found in Strangford Lough, usually on *Modiolus modiolus* (L.) shells. This sea lough is part of the type locality for *brunneus* as specified by Thompson (1840). From this material, a neotype of *O. brunneus* is now described and the status of this taxon discussed. Brief descriptions of *O. lacteus, O. planci* and *Aslia lefevrei* (Barrois) are also given. Apart from material taken in Strangford Lough by the author, specimens of *O. lacteus, planci* and *brunneus* studied were kindly lent by: Miss A. M. Clark of the British Museum (Natural History), London; Mr B. Picton of the Ulster Museum, Belfast, and Dr B. O'Conner of University College, Galway.

Systematic descriptions

Ocnus Forbes & Goodsir in Forbes, 1841

Ocnus brunneus (Forbes *in* Thompson, 1840)

Holothuria brunnea Forbes *in* Thompson, 1840 : 100 (footnote).
Ocnus brunneus: Forbes, 1841; 229–230, fig.
?*Cucumaria brunnea:* Hérouard, 1889 : 682.
?*Cucumaria brunnea*: Koehler, 1921.
Cucumaria lactea (pt.): Mortensen, 1927 : 402–403.
?*Cucumaria planci*: Cherbonnier, 1951 : 39–40.

DIAGNOSIS. Tube feet in single rows; spicules predominantly knobbed buttons with more than four holes; body colour russet brown.

DESCRIPTION. Neotype: BM(NH) reg. no. 1982.7.29.1 Strangford Lough; 15–25 metres. (Figs 1a, 2a–d, 3a). Body length in life, excluding introvert, 7 mm; diameter 2 mm for most of the length, the body truncated. Shrinkage in 70% alcohol was minimal. Fully extended introvert with tentacles almost equal to body length. Tentacles ten, eight long and two ventrally situated ones short. Ambulacra slightly raised, each bearing around ten large tube feet ending in conspicuous suckers, in an almost straight row. Body smooth, rather stiff and angular, pentagonal rather than circular in cross section, posterior end rounded. Spicules very numerous in the body wall and also present in the tube feet and tentacles. In the body wall predominantly knobbed buttons with more than four holes (fig. 2a), tightly packed together; small, almost flat baskets (fig. 2b) superficial to the buttons. Less numerous, but not uncommon, large, smooth fenestrated plates (fig. 2c) also found and in the tentacles smooth fenestrated rods (fig. 2d).

Overall body colour in life a russet brown, fading to greyish brown in spirit; tentacles, posterior end and tube feet creamy white, becoming darker on preservation; the ventral interambulacra a darker brown than the rest of the body. In life small brown bodies noticeable within the tentacle trunks.

The neotype being so small, the description of the internal anatomy which follows has been obtained from other, dissected specimens. When contracted the introvert occupies up to one third of the internal body volume. The retractor muscles are large. One large Polian vesicle is always found. Posterior to the introvert, the gut swells to form a smooth, thick walled stomach—Forbes' 'gizzard'. At the anterior end of the stomach there are a large number of small bodies that are seen as papillae in larger specimens (fig. 3a) but are only brown, warty structures in small specimens. In larger individuals these structures lose their distinctive coloration and are the same creamy-yellow as the rest of the internal anatomy. The gut loops once behind the stomach with a mesentery connecting the ascending and descending sections. In no specimens from Strangford Lough were gonads found and in only one was there evidence of a respiratory tree.

Even in the smallest individuals the knobbed spicules almost invariably have more than four holes, eight being the most common number.

Occasionally individuals of a much lighter brown than the russet commonly encountered were found.

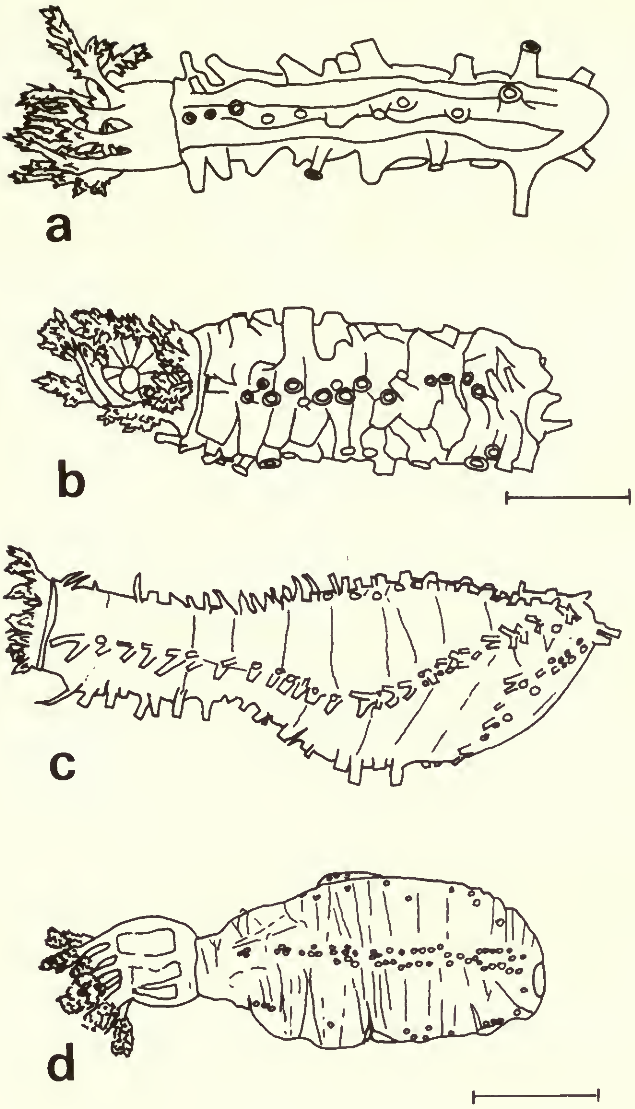

Fig. 1 *Ocnus brunneus* (a) drawn from life, colour russet brown; *O. lacteus* (b) preserved specimen from Strangford Lough, colour white; scale for (a) & (b) 1 mm; *O. planci* (c) preserved specimen from Naples, colour russet brown with faint, darker spots; *Aslia lefevrei* (d) preserved specimen from Garvellachs, Scotland, colour dirty-white to fawn with dark tentacles; scale for (c) & (d) 10 mm.

All the animals examined were dredged from areas of between 15–25 metres in depth, characterized by the presence of the horse mussel *Modiolus modiolus* to whose valves (either alive or dead) specimens were often found adhering. Other holothurian species, including *O. lacteus*, were often taken in the same dredge samples. Captured specimens of *O. brunneus* crawl around aquaria and extend their tentacles regardless of season, suggesting that the species does not hibernate. In the summer months *brunneus* appeared to be more common and individuals larger than in the winter. Similar specimens from Galway and the north-west of Scotland have now been identified as *O. brunneus*.

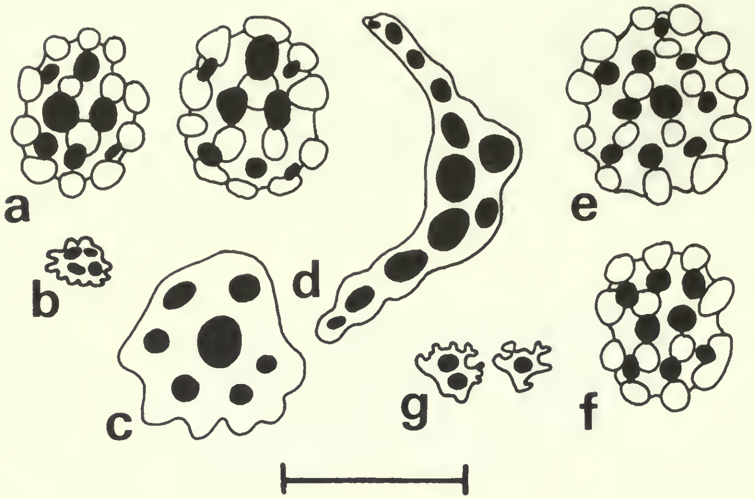

Fig. 2 *Ocnus brunneus* (a) knobbed buttons from the body; (b) flat basket from the body; (c) flat plate from the body; (d) perforated rod from the tentacles. *O. planci* (e) & (f) knobbed buttons from the body; (g) flat baskets from the body. Scale bar 80 µm.

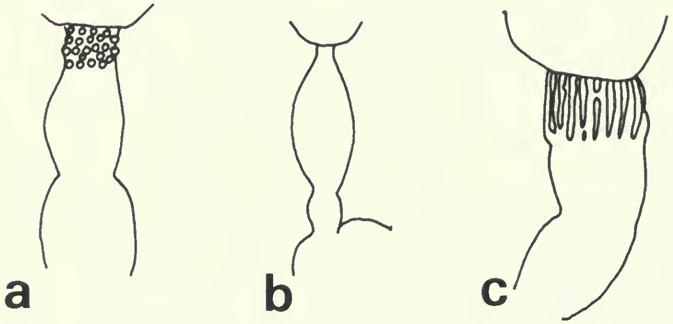

Fig. 3 Stomachs from *Ocnus brunneus* (a); *O. lacteus* (b); *O. planci* (c).

Ocnus planci (Brandt)

Diagnosis. Tube feet in distinct double rows, length up to 15 cm; spicules predominantly knobbed buttons with more than four holes; overall colour russet-brown, sometimes with darker spots; skin relatively smooth. (Figs 1c, 2e–g, 3c)

Ocnus lacteus (Forbes & Goodsir)

Diagnosis. As found in Strangford Lough. Tube feet in single zig-zag rows; length up to 4 cm; spicules predominantly knobbed buttons with four holes, basket spicules almost flat; overall colour brilliant white. (Figs 1b, 3b, 4a–d)

Aslia Rowe

Aslia lefevrei (Barrois)

Diagnosis. Tube feet in double rows but individual tube feet often also found in interradii; length up to 15 cm; spicules predominantly knobbed buttons with four holes, basket spicules very deep in shape; colour from dirty white to black. (Figs 1d, 4f–h)

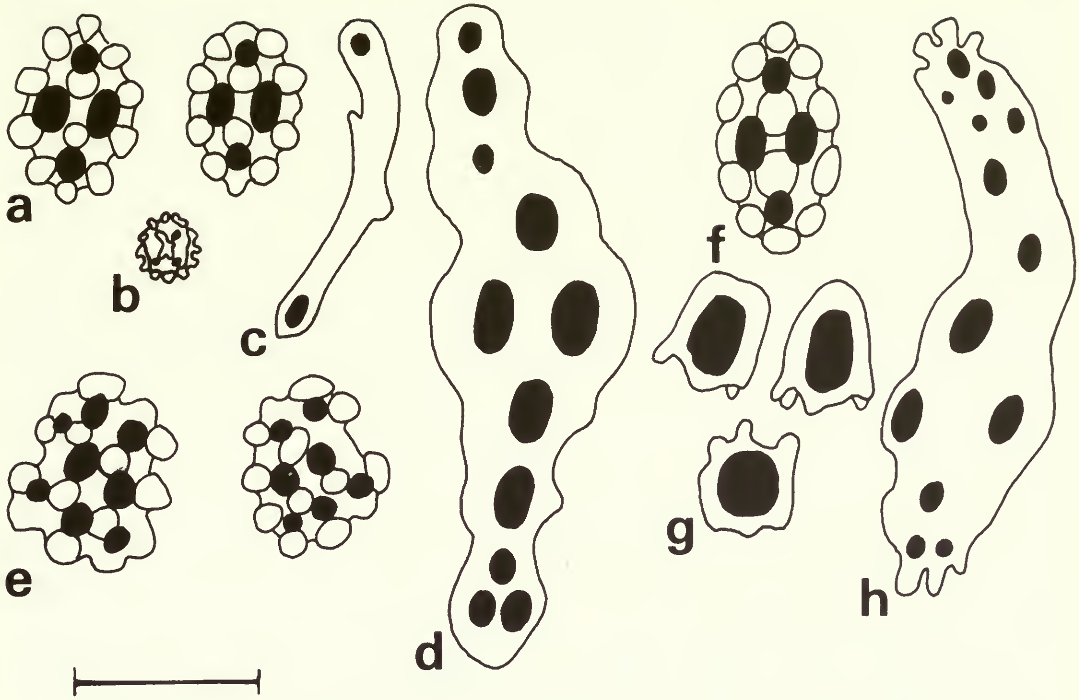

Fig. 4 *Ocnus lacteus* (a) knobbed buttons from the body wall of Strangford specimens; (b) flat basket from body; (c) large rod from body; (d) flat plate from body; (e) knobbed buttons from the body wall of Icelandic (large) specimens. *Aslia lefevrei* (f) knobbed buttons from body; (g) flat plate from body; (h) deep baskets from body. Scale bar 80 µm. N.B. The knobbed buttons of *Aslia* and all the *Ocnus* species may show variation within individuals in the number of perforations in each button but it is the most common button form within an individual that is important in species identification.

Discussion

The illustration of *O. brunneus* and its accompanying text in Forbes (1981) are sufficiently detailed to confirm that the species described above is identical to that described by Forbes. Two possibilities exist as to the status of *brunneus*: either it is a valid species or it is synonymous with another.

While *O. brunneus* is found with *lacteus* in some localities (Hérouard, 1889; pers. obsv.) their geographical ranges differ: *brunneus* extending only to the outer Hebrides of Scotland but *lacteus* being known from as far north as Iceland (Einarsson, 1948). In Strangford Lough the two species are similar in size and, to a lesser extent, in shape but are usually very distinct in colour. The suggestion that Forbes was wrong to recognize two species and that *brunneus* and *lacteus* are synonymous stems entirely from Mortensen (1927). Unfortunately the characters on which this conclusion was based are not discussed; nor does he mention the locality from which his specimens were obtained. His illustrations of the knobbed spicules of *lacteus* show more than four holes, contradicting his description (Mortensen, 1927: Fig. 231 (3)) and suggesting a possible reason for his opinion that the two are synonymous. Strangford specimens of *O. lacteus* of similar size to those of *brunneus* mainly have only four holes in their knobbed plates, these closely resembling the plates found in *Aslia lefevrei.* Large specimens from Iceland which I have named as *lacteus* (Ulster Museum, ZB 234, acc no. Mu 451) have knobbed spicules similar to those illustrated by Mortensen (1927) and are distinguishable from the knobbed plates of *O. brunneus* only in their larger size (Fig. 4e). Interestingly, in the largest of these specimens (>2·5 cm) the tube feet show the suggestion of the formation of double rows though most are still in obviously single, zig-zag rows. Possibly Mortensen compared *brunneus* with large (or Scandinavian?) *lacteus* and assumed that the variation in the plates of *lacteus* would be paralleled in *brunneus.*

The warts and papillae on the stomach of *O. brunneus* were absent from all the specimens of *lacteus* examined (Fig. 3). The single polian vesicle found in *brunneus* may only reflect early development but in *lacteus* of similar size two vesicles were always present. These differences, added to those of colour, indicate strongly that *lacteus* and *brunneus* cannot be considered synonymous.

The only other species of *Ocnus* known from western European waters is *O. planci* (Brandt, 1835) mainly found in the Mediterranean (Koehler, 1921, type locality unknown), though Cherbonnier (1951) recorded it from Belgian waters. In British seas *A. lefevrei* is often misidentified as *O. planci* and I have yet to see an undoubted specimen from the British Isles. If large adults are present in this area then they must be very rare to have escaped the notice of diving naturalists and the dredge. Furthermore, *O. planci* is known to have direct development, without a planktonic stage (Mortensen, 1927). As *planci* has never been recorded from Strangford Lough, and is very unlikely to occur there, it seems improbable that the *brunneus* found there are juvenile *planci.* However, three specimens in a sample collected from Liverpool Bay in 1889 (BM(NH) 89.12.3.40–42) and one from Galway Bay (O'Conner, pers. collection) are intermediate between *brunneus* and *planci,* having spicules indistinguishable from specimens of *brunneus* from Strangford Lough and *planci* from Naples (BM(NH) 98.5.3.252–5) but have, or are forming, double rows of tube-feet while they resemble *brunneus* in shape and colour. The largest of these four specimens is 31 mm long. Gonads are also forming. These intermediates suggest that *brunneus* may be a small form of *planci,* possibly a non-breeding, juvenile form, but, unlike more southern populations, those from the British Isles probably seldom achieve much more than one centimetre in length and only sexually reproduce under ideal conditions. This reproduction could be the source of all the new individuals in the populations but it seems more likely that asexual reproduction makes the major contribution in maintaining local populations. Asexual reproduction through fission is well known in *O. planci* though its contribution to the population biology of this species is unknown (Hyman, 1955). *O. brunneus* is also capable of fission (pers. observ.) and when found on *Modiolus* shells several individuals may be found on the same valve. A specimen of *O. lacteus* in the Ulster Museum is preserved in the act of dividing and is especially interesting in that a smaller individual is dividing from the side of a larger one rather than constricting in the middle and pulling into two halves as has been observed in *brunneus. O. lacteus* is also found on *Modiolus* shells but more usually in dead barnacle shells adhering to the valves. Again two or more individuals are often found in the same barnacle shell. While some other mechanism rather than asexual reproduction could explain such clumping, the importance of fission in the population dynamics of *Ocnus* species deserves further study.

If the *brunneus* populations are self maintaining without the adult *planci* form then there is the very interesting possibility of paedomorphic separation of *brunneus* and *planci. O. lacteus* may represent such a paedomorphically evolved species deriving from a larger form with double rows of tube-feet, similar to *A. lefevrei.* The above does not, of course, preclude the possibility that such separation has already occurred and *brunneus* is already a distinct taxon. At present, however, the evidence is insufficient to allow resolution of this point. Further investigations of *brunneus* are clearly warranted; electrophoresis would be an interesting technique to employ in this and attempts to promote growth of *brunneus* into recognizable *planci* using heated aquaria would be interesting. The relationship between *Ocnus* and the monotypic genus *Aslia* also merits examination.

Acknowledgements

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Three new species of *Varicorhinus* (Pisces, Cyprinidae) from Africa

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Introduction

The genus *Varicorhinus* is contentious and a re-evaluation of it is in preparation. During the course of this work the existence of three new taxa became apparent and to avoid side issues and to make the larger work more coherent, they are described below.

Varicorhinus jubae sp. nov.

A recent sample of 13 fishes from the Juba river, near Sidam, Ethiopia consisted of 10 specimens of *Barbus gananensis* Vinciguerra and three specimens referable to *Varicorhinus*. No species of the latter genus have been recorded from the Juba system.

TYPICAL SERIES. Holotype BMNH 1976.7.1:13; two paratypes BMNH 1976.7.1:14–15, respectively of 135, 101 and 77 mm SL. The fish were collected by Drs Yalden, Largen and Morris from Juba river, close to the Sidam-Bale bridge 05°45′ N, 39°37′ E, altitude 1200 m. The collectors describe the locality as 'permanently flowing river through Acacia woodland. The fish were caught in a shallow stretch where the water flows rapidly over shingle'.

ETYMOLOGY. The specific name alludes to the Juba river and is treated as a feminine Latin noun.

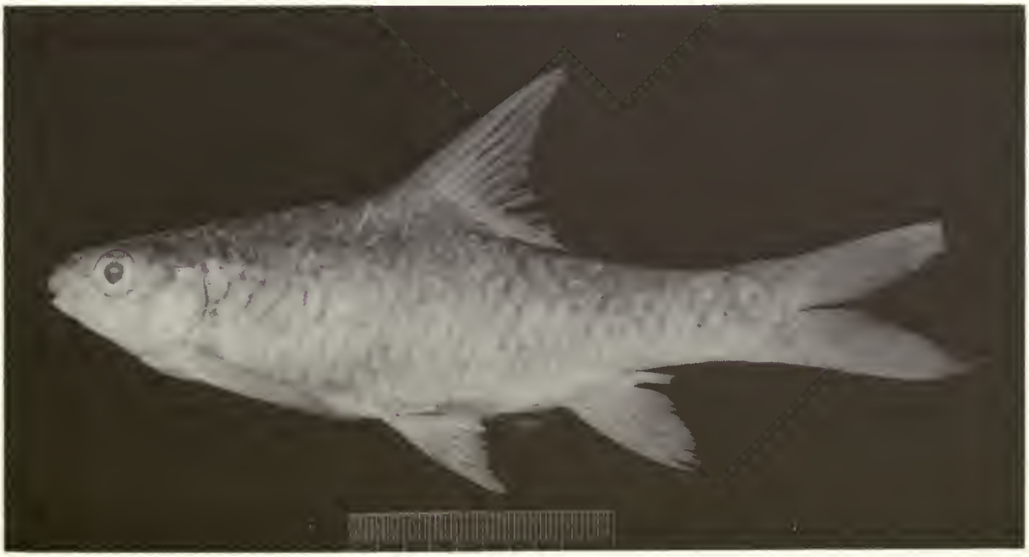

Fig. 1 The holotype of *Varicorhinus jubae*.

Issued 25 October 1984

Description

The description is based on the three fishes noted above. Measurements and abbreviations conform to those detailed in Banister, 1973. Apart from the standard length itself, all figures are a percentage of the standard length.

SL	135 mm	101 mm	77 mm
D	30·6	27·3	26·3
H	23·3	23·3	24·7
I	5·9	6·4	7·3
IO	8·5	7·9	7·6
MW	8·9	7·9	8·6
Pct	23·7	21·8	21·4
Cpl	18·5	19·3	17·8
Cpd	12·2	10·9	11·7
Snt	8·1	7·4	7·2
Ab	2·9	1·9	2·6
Pb	3·7	2·9	4·5
Dsp	31·9	32·6	30·3

The head is short and the snout bluntly rounded. The body is relatively deep and, in the largest specimen, gives the fish the appearance of having been a powerful swimmer. The two smaller specimens are more fusiform. Two pairs of short barbels are present. Small, off-white tubercles are distributed over the sides of the snout in all three fishes.

The mouth is wide and ventral. The lower jaw is short, its anterior edge gently curved and covered with a sharp-edged horny sheath (Fig. 2). The 101 mm SL specimen has a gut length of 200 mm (the same length as in a sympatric *Barbus gananensis* of 103 mm SL). All the specimens are either sexually immature or quiescent. There are 39(f1) or 40(f2) vertebrae including those of the Weberian mechanism.

Dorsal fin. There are four unbranched and 10 branched rays (f3). The last unbranched ray is ossified into a stout, straight, smooth spine. When erect, the dorsal margin of the fin is concave. A low sheath of scales envelops the base of the fin. The first ray is in advance of the vertical from the pelvic fin origin.

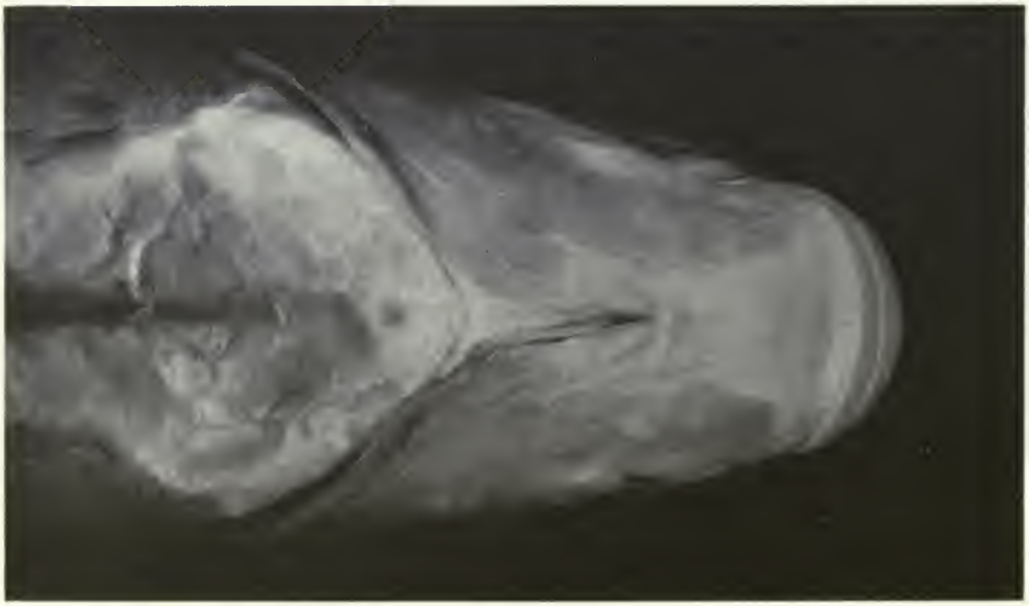

Fig. 2 Ventral view of the head of the holotype of *Varicorhinus jubae.*

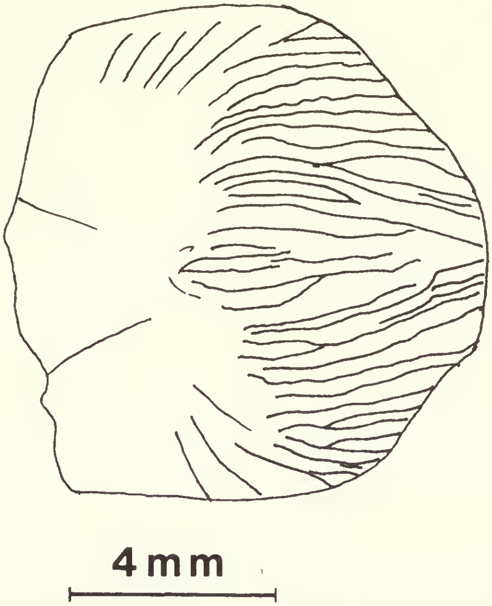

Fig. 3 The striations of the fifth scale from the row above the lateral line of the holotype.

The *Anal fin* has three unbranched and five branched rays (f3). The last branched ray of the holotype is split to the base giving the appearance of a sixth ray.

Squamation. In the lateral line series there are 26, 27 and 31 scales. From the dorsal mid-line to the lateral line there are $4\frac{1}{2}$ (f3) scales and from there to the ventral mid-line also $4\frac{1}{2}$ (f3) scales. There are 12 (f3) scales around the least circumference of the caudal peduncle. Between the lateral line and the pelvic fin base there are $1\frac{1}{2}$ (f2) or $2\frac{1}{2}$ scales. The pattern of the scale striations is shown in Fig. 3.

Pharyngeal bones and teeth. The pharyngeal teeth number 2.3.5–5.3.2 (f3). The pharyngeal bone is depicted in Fig. 4 where it can be seen that it is smaller than that of an equivalently sized *Barbus gananensis.*

Gill rakers. On the lower limb of the first gill arch there are 16 (f1) or 17 (f2) long, hooked gill rakers.

Coloration. Alcohol preserved specimens are dark grey-brown dorsally, silver-grey laterally and pale grey ventrally. The fins are pale grey. In life, the fishes were intensely silver, darkening dorsally.

Distribution. This species is known only from the type locality.

Comparison with Barbus gananensis

The last re-description of *Barbus gananensis* (Banister, 1973) was based on only three long-preserved specimens so the extra ten specimens mentioned above (BMNH 1976.7.1:3–12) were very useful. These specimens 71 mm to 125 mm SL have shallower caudal peduncles (11·0–12·9 *cf* 13·1–15·0% SL) than the previous sample as well as fewer lateral line scales (26 (f5), 27 (f3), 28 (f1) and 29 (f1) *cf* 29 (f2) or 31 (f1) suggesting that the previously reported range may be atypical. All other counts and measurements lie within the published limits but the head length, snout length and the length of both pairs of barbels lie at the upper ends of the ranges.

In overall appearance, *Varicorhinus jubae* and *Barbus gananensis* resemble each other more closely than either does its respective congeners. Although such resemblances are unquantifiable, the reality can be seen by comparing Figs 1 & 6. The head is excluded from these comments.

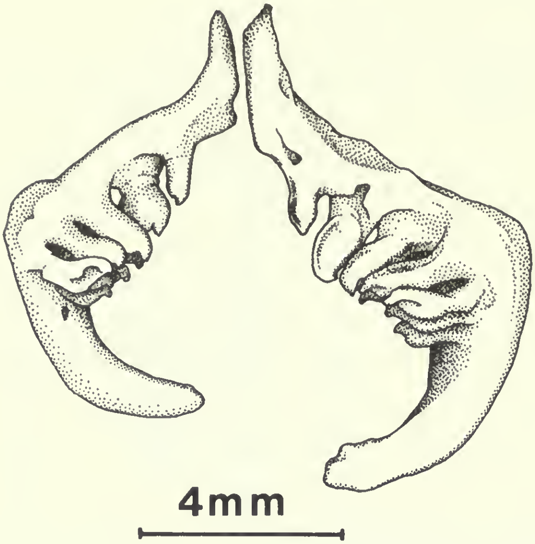

Fig. 4 Comparison of the pharyngeal bones of *Varicorhinus jubae* 101 mm SL (left), and *Barbus gananensis* 103 mm SL.

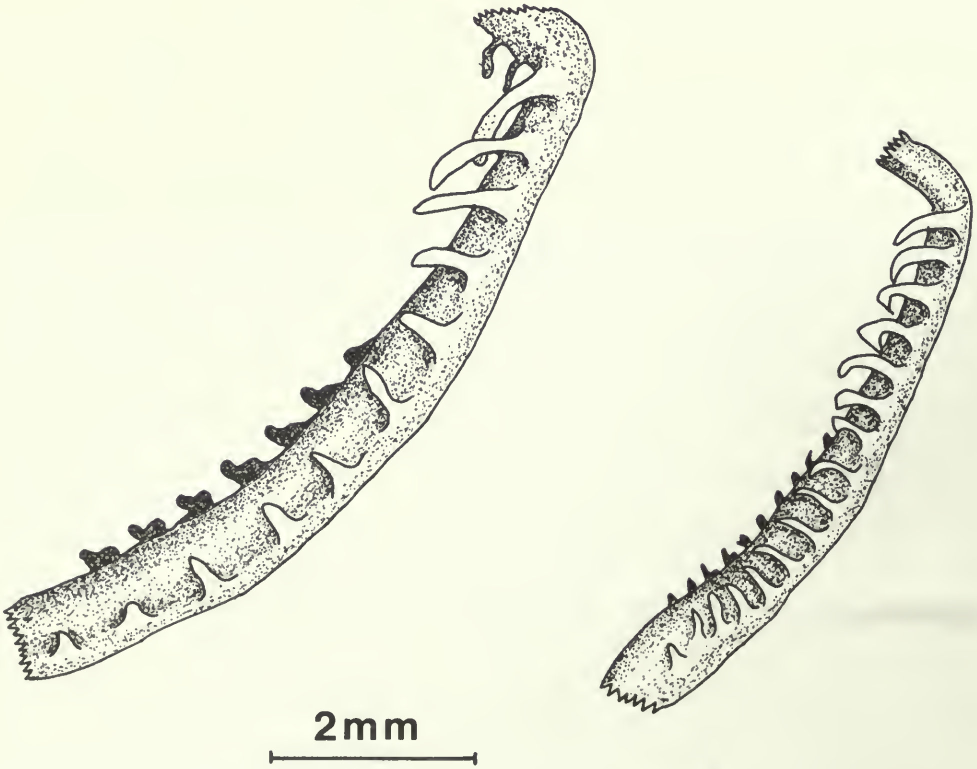

Fig. 5 The gill rakers on the first ceratobranchial of *Barbus gananensis* (A) 103 mm SL, and *Varicorhinus jubae* (B) 101 mm SL.

The most conspicuous differences between *V. jubae* and *B. gananensis* occur in characters related to feeding. The wide mouth, sharp edge to the lower jaw, smaller barbels and higher number of gill rakers in the new species are all characters that are associated with scraping, epilithic dietary habits. The disparity in the pharyngeal bone size has been noted above and further discussed in Banister, 1972.

The presence of a *Varicorhinus* species bearing a close superficial resemblance to a sympatric *Barbus* species has been observed in other instances. *Varicorhinus ruwenzorii* from the Ruimi river, Uganda, has the same striking colour pattern as *Barbus somereni* (Banister, 1972). From the Upemba region of Zaire a similar pairing phenomenon is shown by *Varicorhinus upembensis* and *Barbus gestetneri* (Banister & Bailey, 1979). Although I have no immediate explanation for this, the phenomenon will be treated in detail in the reassessment of the genus referred to above.

Varicorhinus clarkeae sp. nov.

HOLOTYPE. A fish of 151 mm SL, No. 164456 in the Musée Royale de l'Afrique Centrale, Tervuren, Belgium. Specimen No. 164457 is designated a paratype. Both specimens (previously registered as *Varicorhinus ensifer*) were collected in the Rio Cunje, an affluent of the Cuanza, Ceilunga, Angola.

ETYMOLOGY. Named in honour of Mrs Margaret Clarke who gave so much assistance during the course of these researches.

Description

Based on the two specimens of 151 and 161 mm SL. The morphometric data (holotype first) is as follows: D=22·5, 23·6; H=20·5, 20·5; I=4·0, 6·3; IO=8·0, 7·5; MW=7·3, 6·8; Pct=19·3; 18·6; Cpl=14·6, 18·0; Cpd=9·3, 10·6; Snt=7·3, 6·8; Ab=1·7, 1·0; Pb=3·6, 2·5; Dfin=21·8, 18·0.

The body is shallow and nearly circular in cross section. The lower jaw has a slightly curved anterior edge is covered with a thin horny layer. Papillae are present on both lips, those on the upper lip decrease in size anteriorly and are larger than those on the lower jaw which are confined to a strip behind the horny sheath. The snout is fleshy and a thin

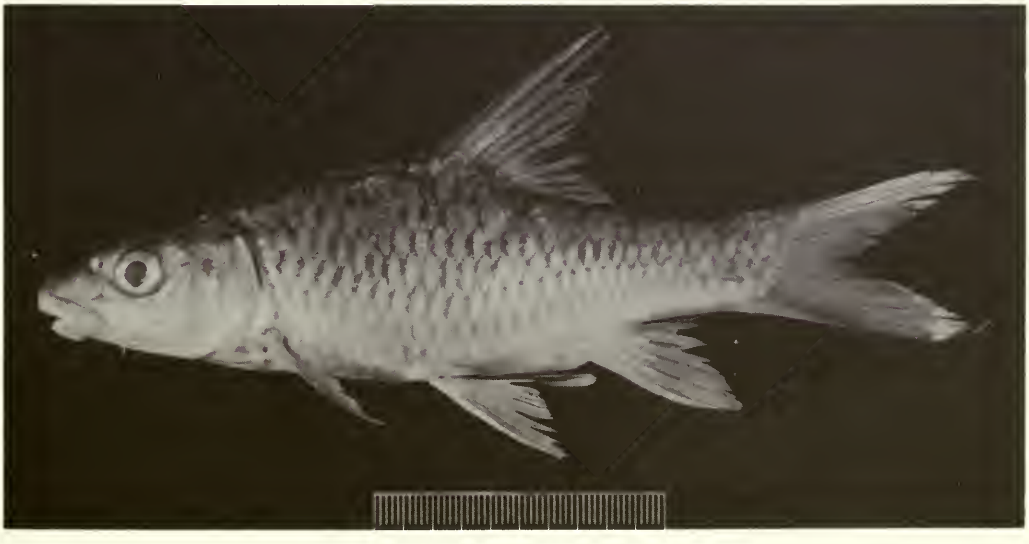

Fig. 6 *Barbus gananensis* 103 mm SL.

ventral flap covers the anterior edge of the upper jaw. There are no tubercles nor tubercle scars on the snout but what could be scars of small tubercles are present on the skin covering the lachrymal bone in the holotype. Two pairs of small barbels are present. There are 41(f2) vertebrae, including those of Weberian mechanism.

Dorsal fin. There are 4 unbranched and 9 branched rays (f2). The last unbranched ray is ossified into a thin, short, straight spine. There is no raised sheath of scales around the base of the dorsal fin.

The *Anal fin* has three unbranched and five branched rays (f2).

Squamation. The lateral line has 33 or 35 scales and is relatively high on the body (see below). There are 5½ (f2) scales between the dorsal mid-line and the lateral line and 5½ (f2) from there to the ventral mid-line. Three scales lie between the lateral line and the pelvic fin (f2). Twelve scales encircle the least circumference of the caudal peduncle. The scale striations are parallel.

Gill rakers. There are 16 gill rakers on the lower limb of the first gill arch of the holotype.

Pharyngeal bones and teeth. The pharyngeal teeth number 2.3.5–5.3.2. The posterior faces of the crown of the second and third teeth of the inner row (I2 & I3 in the system of Banister & Clarke, 1980) have a horseshoe shaped ridge which becomes exaggerated on I4, I5, II2 and II3.

Coloration. In alcohol preserved specimens the back is dark brown, the belly and flanks lighter brown. The demarcation between the two browns is very marked on the posterior part of the fish.

DISTRIBUTION. Known only from Cunaza, Ceilunga, Angola, approximately 12°00′ S, 17°40′ E.

Diagnosis and affinities

The presence of papillae on the lips and a horny edge to the lower jaw suggests an affinity with *Varicorhinus ensifer* Boulenger and the species described below as this combination of features appears to be unique to these three species. *Varicorhinus clarkeae* can be distinguished from *V. ensifer* by a shorter, thinner dorsal fin spine and a more cylindrical body.

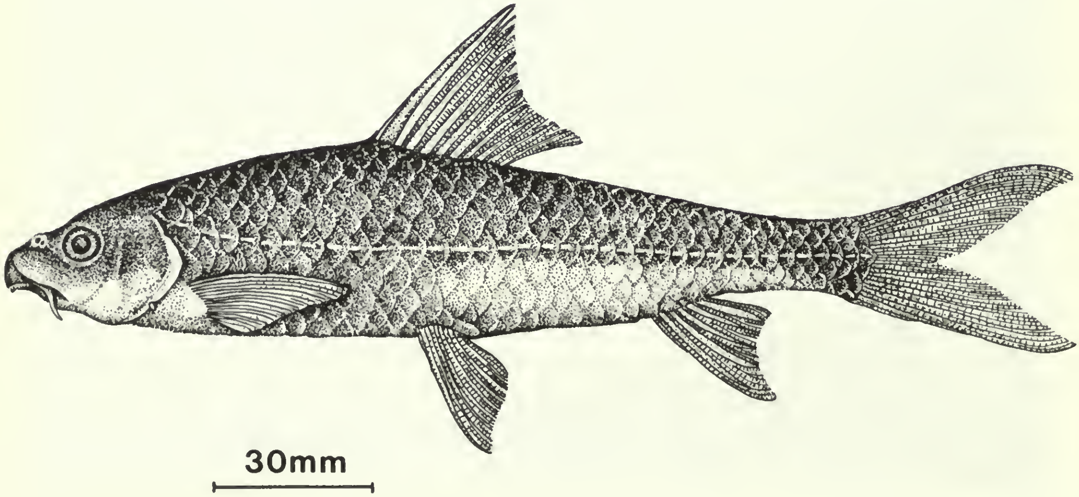

Fig. 7 *Varicorhinus clarkeae* the holotype.

Varicorhinus robertsi sp. nov.

TYPICAL SERIES. Holotype, a fish of 65 mm SL from the Sanga waterfalls at the tailwaters of the hydroelectric dam at Sanga on the Inkisi river, Zaire, BMNH 1983.3.30:20; paratypes 18 specimens 38·7–64·0 mm SL from the same locality, BMNH 1983.3..30.21–38. All the specimens were collected by Drs Tyson Roberts and Don Stewart on June 26 1973.

ETYMOLOGY. Named after the ichthyologist and collector Dr Tyson Roberts.

Description

The description is based on the 19 specimens listed above.

	x̄	s.d	s.e.	range mm
L				38·7–65·0
D	26·0	1·3	0·3	24·1–28·8
H	25·8	1·1	0·3	23·4–27·8
I	7·0	0·9	0·2	5·9– 8·4
IO	6·2	0·6	0·1	5·2– 7·4
MW	5·8	1·0	0·2	5·9– 9·6
Pct	22·1	1·0	0·2	20·2–24·2
Cpl	17·7	1·3	0·3	15·5–20·8
Cpd	10·5	0·5	0·1	9·4–11·7
Snt	8·4	0·5	0·1	7·6– 9·4
Ab	+	–	–	–
Pb	2·3	0·3	0·1	1·6– 2·7
Dfin	29·1	2·6	0·6	25·2–34·4

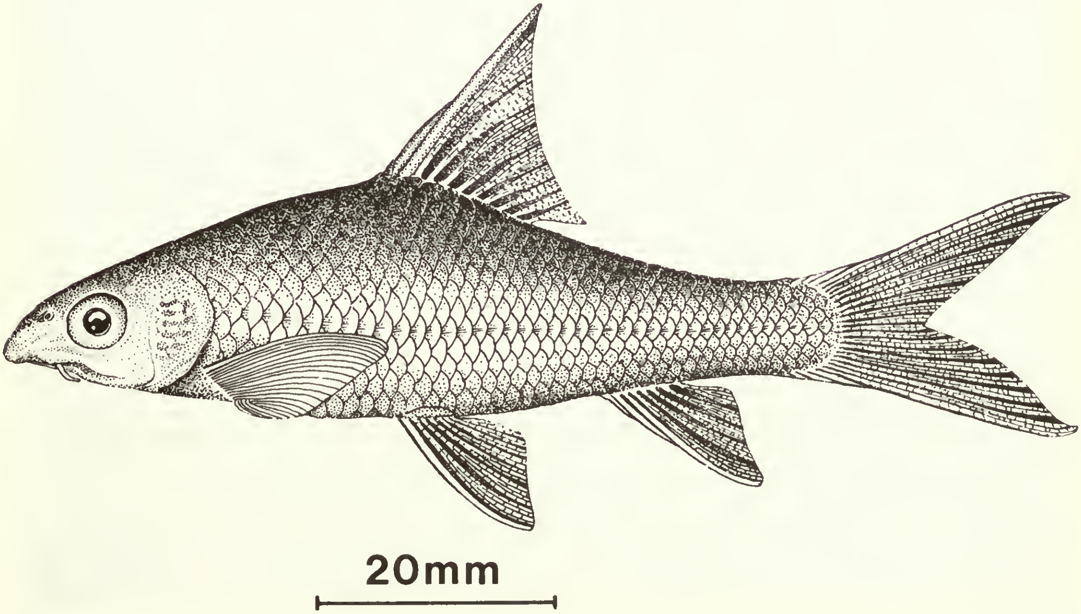

Fig. 8 *Varicorhinus robertsi* the holotype.

A further 9 specimens were collected (18·4–38·7 mm SL) but are not included in this description because their poor condition precluded accurate measurement.

The body is compressed, its greatest depth is immediately in front of the dorsal fin. The dorsal profile is more convex than the ventral profile. The snout is fleshy, rounded and extends in front of the mouth. The ventral face of the head is concave just behind the mouth. The upper jaw bears rows of papillae (Fig. 9), one row appears on the lip of small fishes (*circa* 30 mm SL) and the number of rows increases with size. The lower jaw has papillae behind the sharp-edged horny sheath. None of the specimens has tubercules. There are minute anterior barbels. In the ten specimens radiographed there are 38 (f1), 39 (f5) or 40 (f4) vertebrae including those of the Weberian mechanism.

Dorsal fin. There are 4 (f19) unbranched and 8 (f2) or 9 (f17) branched rays. The last simple ray is formed into a thin, smooth spine. The dorsal fin origin is anterior to that of the pelvic fin. The *anal fin has* 3 unbranched and 5 (f19) branched rays.

Squamation. In the lateral line there are 39 (f9), 40 (f5), 41 (f4) or 43 (f1) scales. From the dorsal mid-line to the lateral line there are 6½ (f12) or 7½ (f5) scales and from there to the ventral mid-line 6½ (f4) or 7½ (f14) scales. Between the lateral line and the pelvic fin base there are 4 (f4), 4½ (f13) or 4 (f2) scales. Eighteen (f1) or 16 (f16) scales encircle the least circumference of the caudal peduncle. Scale counts were not obtainable on all specimens. There are few striations on the scales and their disposition is shown in Fig. 10.

Pharyngeal bones and teeth. The teeth number 2.3.5–5.3.2. The last tooth on the inner row (I5) has a conspicuous sulcus on the crown in the plane of the tooth. The pharyngeal bone is shown in Fig. 11.

Gill rakers. There are 10 (f1), 11 (f3) or 12 (f3) on the lower limb of the first gill arch in the 7 specimens examined.

Coloration. The body colour in alcohol preserved specimens is pale brown, only slightly darker on the back than on the belly. A narrow, dark strip covers the ridge of the back from

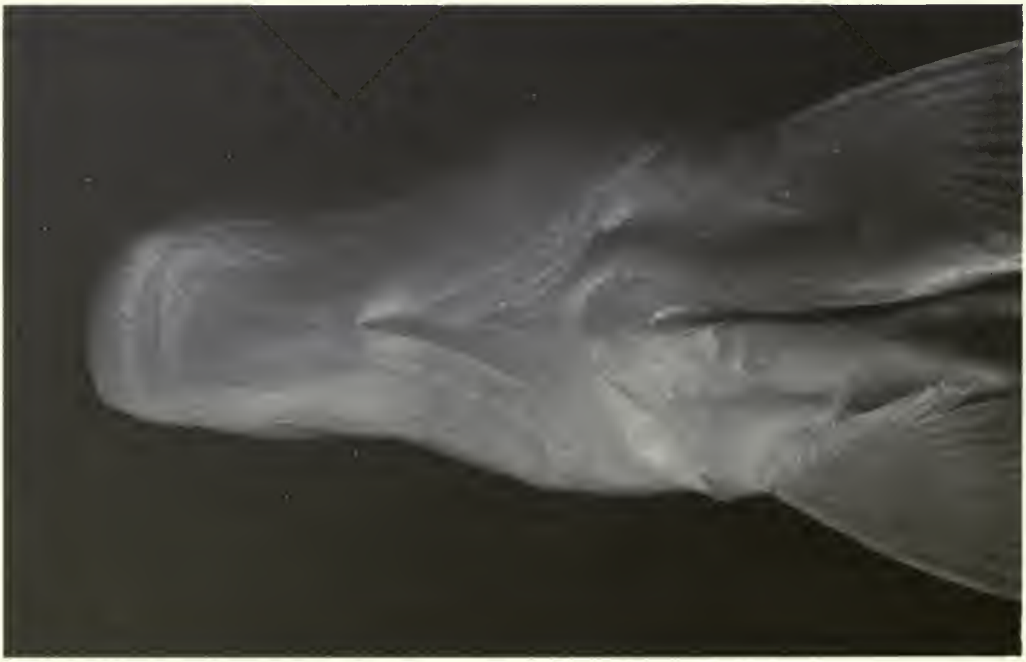

Fig. 9 Ventral view of the head of the holotype of *Varicorhinus robertsi* to show the papillae.

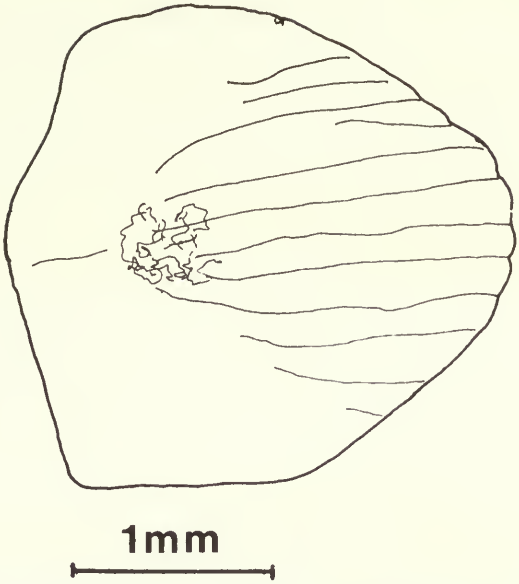

Fig. 10 The fifth scale from the row above the lateral line of the holotype of *Varicorhinus robertsi.*

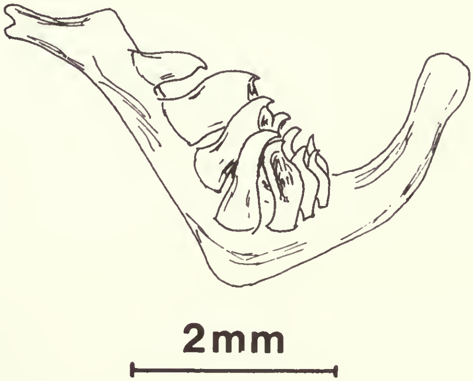

Fig. 11 *Varicorhinus robertsi* pharyngeal bone from the largest paratype.

the occipital region to the dorsal fin origin. The smaller specimens have a dark spot at the base of the tail fin. The centre of the operculum is transparent and the gills are visible through it. The paired fins are hyaline. The caudal fin lobes have a streak of dark pigment and the dorsal fin has a dark, dorsal margin. The live colour is unknown.

Distribution. This species is known only from the type locality, the Sanga waterfalls, 4°50′ S, 14°47′ E. Zaire.

Diagnosis. From the other *Varicorhinus* species with papillae on the lips this species is easily distinguished by the presence of smaller scales.

Acknowledgements

Firstly, I wish to thank the collectors for their care in preserving and bringing back the specimens. Secondly, I would like to thank my colleagues, Dr P. H. Greenwood, Mr G. J. Howes and Mrs Margaret Clarke for their help and advice. The drawings are the work of Jack Shroeder (7), Mandy Holloway (8) and Gordon Howes: to them and the photographer, Mr Paul Richens, I extend my thanks. I am very grateful to Ms Julie Hacker for typing the manuscript.

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Phyletics and biogeography of the aspinine cyprinid fishes

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Introduction

This study was initiated by the examination of specimens of the Hwang-Ho dace, *Leuciscus mongolicus* (Kessler, 1876) in the collections of the American Museum of Natural History. Even a cursory examination cast doubt on their assignment to the genus *Leuciscus*, and a more detailed anatomical study, reported herein, indicates that the species should be allocated to a new genus. Study of this material has also led to a reappraisal of the genus *Leuciscus* and to a discussion of the phyletics and zoogeography of the aspinine cyprinids.

Methods and materials

As in previous studies (Howes, 1978, 1980, 1981) a wide range of both barbelled and non-barbelled Old World cyprinids have been examined. The materials listed in those papers have been re-examined together with more recently prepared material. In addition, skeletal preparations of many Nearctic taxa have also been studied. The following species were dissected, or skeletal preparations examined.

Abramis brama; *Algansea tincella*; *Aspiolucius esocinus*; *Aspiopsis merzbacheri*; *Aspius aspius*; *Aspius vorax*; *Chondrostoma nasus*; *Elopichthys bambusa*; *Gila bicolor*; *G. copei*; *G. crassicauda*; *G. cypha*; *G. elegans*; *G. nigrescens*; *G. pandora*; *G. robusta* (these include Michigan Museum specimens); *Lavinia exilicauda*; *Leuciscus borysthenicus*; *L. cephalus*; *L. idus*; *L. fellowesii*; *L. lehmanni*; *L. leuciscus*; *L. orientalis*; *L. schmidtii*; *L. smyrnaeus*; *L. souffia*; *L. svallizae*; *L. waleckii* (including the syntypes of *L. waleckii sinensis* in the Swedish Museum of Natural History); *Luciobrama macrocephalus; Mylocheilus caurinus*; *Ochetobius elongatus*; *Oreoleuciscus humilis*; *O. pewzowi*; *O. potanini*; *Orthodon microlepidotus*; *Pelecus cultratus*; *Pogonichthys macrolepidotus*; *Ptychocheilus lucius; P. grandis*; *P. oregonensis*; *Rhynchocypris variegatus*; *Tinca tinca*; *Tribolodon brandti*; *T. jouyi*; *Xenocypris argenteus.*

The concept of *Leuciscus* and the status of *Leuciscus mongolicus* (Kessler)

The daces and chubs of the genus *Leuciscus* Cuvier, 1817 form the most speciose group of Palearctic cyprinid fishes, there being at least 36 nominal species (the number listed in the BMNH catalogues). The majority of *Leuciscus* species are alike in having moderately deep and stout bodies, broad cranial bones (including the ethmoid and supraorbital), a ventrally directed basioccipital process with a well-formed masticatory plate, biserially arranged uncinate pharyngeal teeth, and a short-based anal fin. Comparative studies (Howes, 1978, 1980, 1981) suggest that these 'diagnostic' characters are plesiomorphic for non-barbelled cyprinids. *Leuciscus,* as presently recognized, cannot be defined by a set of unique characters and is therefore a non-monophyletic assemblage.

One species of *'Leuciscus'*, *L. mongolicus* (Kessler, 1876), has, however, a suite of derived characters that sets it apart from the corpus of *Leuciscus* species (detailed in Table I). Some of these specializations are shared with genera of the *aspinine group sensu* Howes, 1978 (see pp. 291 below) and are as follows:

Bull. Br. Mus. nat. Hist. (Zool.) **47**(5): 283–303 Issued 25 October 1984

Table 1

Character	*Leuciscus* spp.	*'Leuciscus' mongolicus*
Cranial width	40%	61%
(% of its length from tip of ethmoid indentation to the posterior border of the superaoccipital)	mode of 20 specs representing 6 species (110–230 mm SL)	mode of 9 specs (72–147 mm SL)
Supraethmoid	with slightly concave lateral border	narrow-waisted
Mesethmoid	deep with wide anterior notch	shallow with V-shaped notch
Maxillary mid-lateral ascending process	low	high
Dentary pores	5–6	8
Pterosphenoid	short, lacking shelf and remote from frontal border	elongate, with lateral shelf and extended to the frontal border
Orbitosphenoid keel	deep	shallow
Basioccipital process	ventrally sloped	horizontal
Dilatator fossa	short, sphenotic with straight posterior border	long, sphenotic with concave posterior border
Epioccipital process	short, rounded	extended, triangular
4th infraorbital canal	follows contour of orbit	divergent from orbital border
Operculum	dorsal border short, posterior border rounded	dorsal border long, posterior border concave in outline
Adductor arcus palatini muscle originates from:	parasphenoid and prootic	pterosphenoid, parasphenoid and prootic
Gill-rakers	few, stout and simple	many, slender with a crenate medial membrane
Gap between branchial arch and bucco-pharyngeal roof	restricted (Fig. 11)	extensive (Fig. 11)
Genital papilla	not pronounced	elongate, with deeply folded border

The cranium of *'Leuciscus' mongolicus* more closely resembles that of *Aspius* than that of any other *Leuciscus* species (Fig. 1). This resemblance is due to its narrowness, particularly that of the suprathemoid and the frontals which are markedly concave above the orbit; extension of the posterior border of the epioccipital; extent of the dilatator fossa; width of the pterosphenoid; shallowness of the orbitosphenoid keel and the horizontal plane of the basioccipital process.

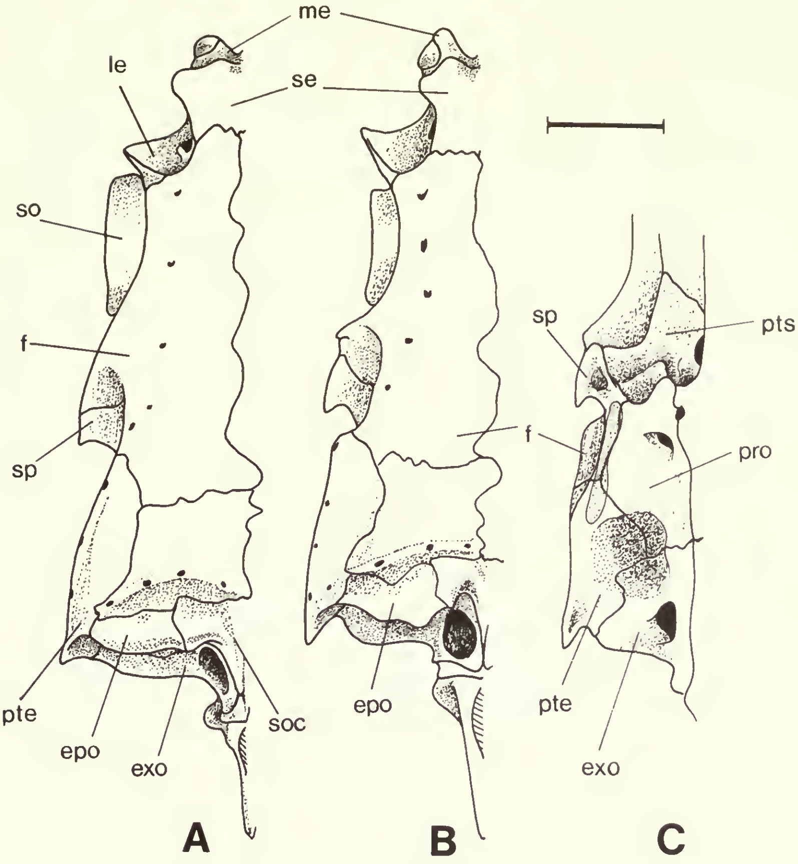

Fig. 1 Crania of A, *Leuciscus leuciscus;* B and C, *Genghis mongolicus.* A and B in dorsal, C in ventral views. Scale = 5 mm. epo = epioccipital, exo = exoccipital, f = frontal, le = lateral ethmoid, me = mesethmoid, pro = prootic, pte = pterotic, pts = pterosphenoid, se = supraethmoid, so = supraorbital, soc = supraoccipital, sp = sphenotic.

Cranial width varies in cyprinids and cannot, by itself, be treated as a synapomorphy. However, among the aspinine genera (*Aspius, Elopichthys, Pseudaspius, Aspiolucius* and *Luciobrama*; Howes, 1978) there is, associated with a narrow cranium, marked concavity of the frontal border above the orbit and an elongate ethmoid region. The lateral margin of the supraethmoid is deeply concave and the mesethmoid arms prominently extended forming a V-shaped anterior notch. All these features are characteristic of *'Leuciscus' mongolicus* (Figs 1 & 2).

An aspinine synapomorphy (Howes, 1978) is the posterior extension of the epioccipital which, in combination with the lengthened parietal and flattened lateral portion of the supraethmoid, forms an occipital platform (postcranial platform of Howes, 1978). In '*Leuciscus' mongolicus* the occipital platform is not developed to the extent that it is in aspinine genera, but nonetheless this feature is absent in *Leuciscus* species.

The dilatator fossa in *'Leuciscus' mongolicus* makes a deep excavation into the frontal (Fig. 1B); the sphenotic is expanded posteriorly with a deeply concave posterior margin. This fossa morphology is unlike that in other *Leuciscus* species where the frontal is only shallowly indented and the sphenotic is short with, at best, a slightly concave posterior border. A long, deep indentation of the frontal and a deeply concave sphenotic are characteristics of the aspinine dilatator fossa (see Howes, 1978, figs 25 & 26).

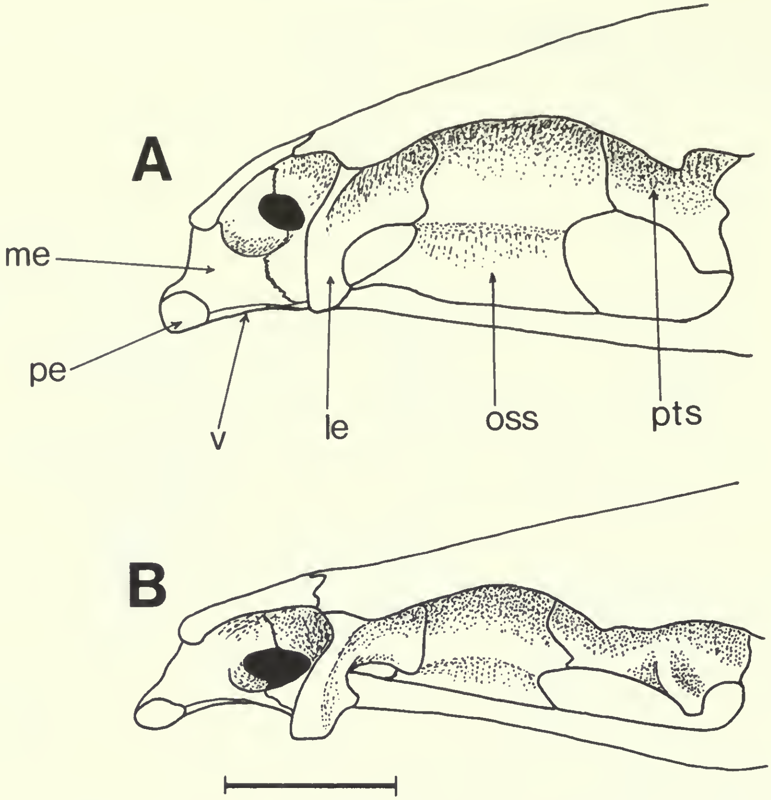

Fig. 2 Anterior cranial region of A, *Leuciscus leuciscus* and B, *Genghis mongolicus* in lateral views. Scale = 5 mm. oss = orbitosphenoid 'septum', pe = preethmoid, v = vomer; other abbreviations as in Fig. 1.

The lateral extension of the pterosphenoid is an aspinine synapomorphy, a feature most marked in *Aspius* and *Elopichthys*. The most extreme pterosphenoid expansion occurs in *Elopichthys* where the bone is also exposed dorsally and forms the site of origin for part of the *adductor mandibulae* musculature (see Howes, 1978: 32 & 53). In *'Leuciscus' mongolicus* the pterosphenoid is narrowly separated from the margin of the overlying frontal and resembles the condition in *Aspius* (cf Fig. 1B with fig. 27B in Howes, 1978). As in the aspinine genera, the pterosphenoid is elongate, being longer than the orbitosphenoid and having a prominent, downwardly curved lateral shelf (Fig. 2B). The usual cyprinid condition is for the orbitosphenoid and pterosphenoid to be of equal length or for the pterosphenoid to be shorter and without a lateral shelf. The orbitosphenoids in *'Leuciscus' mongolicus* are joined to the parasphenoid by a shallow keel or 'septum', thus contrasting with the condition in other *Leuciscus* species where a deep keel is present (Fig. 2A). Again, this condition resembles that of the aspinines where contact between the orbito- and parasphenoid is direct or *via* a shallow keel (see Howes, 1978:31). The anterior myodome in *'Leuciscus' mongolicus* has suffered reduction as a consequence of the depressed anterior part of the cranium. In other *Leuciscus* species the myodome is a spacious cavity.

In the arrangement of its infraorbital bones, *'Leuciscus' mongolicus* resembles the aspinines more closely than it does other *Leuciscus* species (Fig. 3A). Synapomorphic for aspinine genera is the elongate 3rd infraorbital, the wide separation of the 4th infraorbital from the orbital border, and its divergent angle (Howes, 1978, fig. 20). In *'Leuciscus' mongolicus* there is a similar elongation of the 3rd infraorbital and a divergent

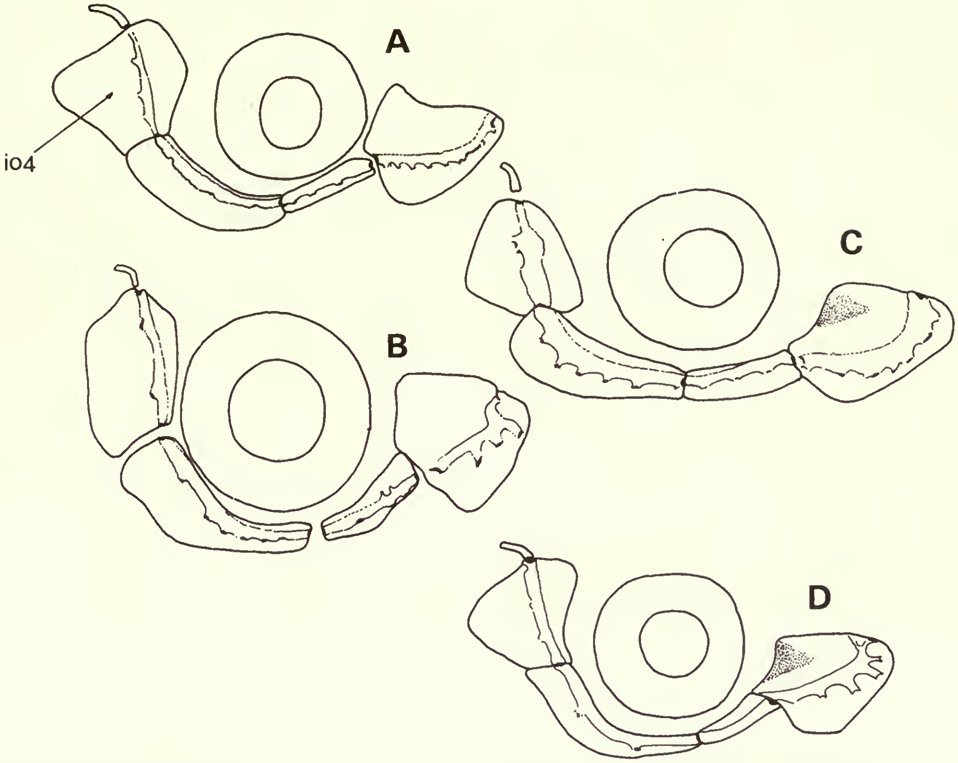

Fig. 3 Infraorbital series of A, *Genghis mongolicus*; B, *Leuciscus leuciscus*; C, *Aspiopsis merzbacheri*; D, *Tribolodon brandti.*

4th element. *Leuciscus* species, in common with most cyprinids, have the 4th infraorbital canal in a near vertical alignment and following the contour of the orbital border (see Howes, 1978, fig. 21). The posterior extent of the bone is variable. What may represent the plesiomorphic condition is illustrated in bariliines (Howes, 1980, figs 29A & B). In these taxa the 4th infraorbital canal also takes a near vertical course and the lamellar part of the bone covers the adductor musculature. In aspinines and *'Leuciscus' mongolicus* the 4th infraorbital is also expanded, its posterior margin being attenuated, but the canal runs through the centre of the bone at a divergent angle to the orbit (Fig. 3A). This particular configuration of the infraorbital in the aspinines and *'Leuciscus' mongolicus* is a correlate of the elongated posterior cranial bones, particularly the pterosphenoid. The result has been a backward shift of the pterotic-infraorbital canal commissure and a re-alignment of the 4th and 5th infraorbital canals.

The arrangement of the *adductor arcus palatini* (AAP) musculature in *'Leuciscus' mongolicus* differs from that of other *Leuciscus* species in having its origin not only from the more usual sites *viz* the prootic and parasphenoid, but also from the pterosphenoid. The anterior part of the muscle originates tendinously from the prominent lateral pterosphenoid shelf and the lateral surface of the parasphenoid ascending process. Insertion of the muscle is on to the lateral face of the posterior margin of the entopterygoid and the entire dorso-lateral face of the metapterygoid (Fig. 4A). The muscle is thick and convex; posteriorly it is confluent with the *adductor hyomandibularis* which runs from the prootic to the medial face of the hyomandibula.

In *Leuciscus* species and the majority of cyprinids, the AAP extends from the base of the neurocranial part of the parasphenoid to its orbital portion. Often, the muscle is continuous with the *adductor hyomandibularis* which originates from the posterior part of the prootic.

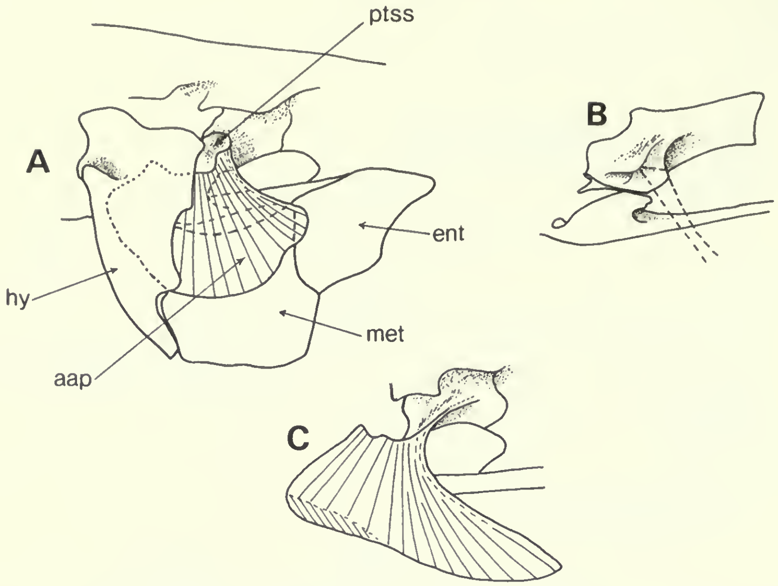

Fig. 4 Origins and insertions of the *adductor arcus palatini* muscle in A, *Genghis mongolicus*; B, *Oreoleuciscus pewzowi* and C, *Pogonichthys macrolepidotus,* lateral views. In A, the dotted line indicates area of origin of the 'adductor hyomandibularis' portion of the muscle from the cranium; the dash-dot line, its insertion on the hyomandibula. In B, the tendinous origin of the muscle is indicated by dashed lines. aap = *adductor arcus palatini* muscle, ent = entopterygoid, hy = hyomandibula, met = metapterygoid, ptss = pterosphenoid shelf.

In cyprinids investigated, only in genera of the aspinine group (except *Luciobrama* which lacks an AAP; see Howes, 1978:24), and in *Oreoleuciscus, Tribolodon* and *Pogonichthys* does the AAP originate from the pterosphenoid. For these taxa the condition is considered to be synapomorphic.

There are 3–4 gill-rakers in *'Leuciscus' mongolicus* on the 1st epibranchial, with 8–9 on the outer and 12 on the inner side of the 1st ceratobranchial. Those on the inner side closely intermesh with the 13 or so rakers on the outer edge of the 2nd ceratobranchial. The gill-rakers are well-developed with a strong, triangular bony spine supporting a thin medial mucosal membrane, the border of which is convex and crenate. The membrane is most developed on the posterior rakers of the ceratobranchial (Fig. 5A). In *Leuciscus leuciscus* and the majority of its congeners, the bony core of the gill-raker is a short, flat, almost equilateral triangle invested by mucosal tissue. This is in contrast to the '*L.*' *mongolicus* morphotype, where the bony part of the raker is exposed laterally.

Berg's (1949) diagnosis of *Leuciscus* gives gill-rakers as 'short, few (6–30)'; in his key there are three species with more than 13 rakers, *viz. bergi, lindbergi* and *schmidtii.* No specimens of the two former species are available to me, but in *L. schmidtii* the posterior gill-rakers are of the same morphotype as in *'L.' mongolicus.* Gill-rakers with a crenate border to the medial membrane are present also in genera of the *aspinine group* and in *Aspiopsis, Tribolodon, Oreoleuciscus* and *Pogonichthys.* Comprison of gill-raker types in several cyprinid taxa has shown that this form of raker is comparatively rare. Normally the mucosal membrane has a plain concave border, but in some taxa, e.g. *Cyprinus*, the rakers have a thick and highly folded mucosal membrane. Dendritic and pulvinate gill-raker membranes are also common, the tissue often papillose as in abramines. However, in these taxa the pulvinate membrane meets a thick longitudinal septum (see Zander, 1903 for description of *Abramis*) and the rakers lie close together so that the fimbriate medial margins form a sieve.

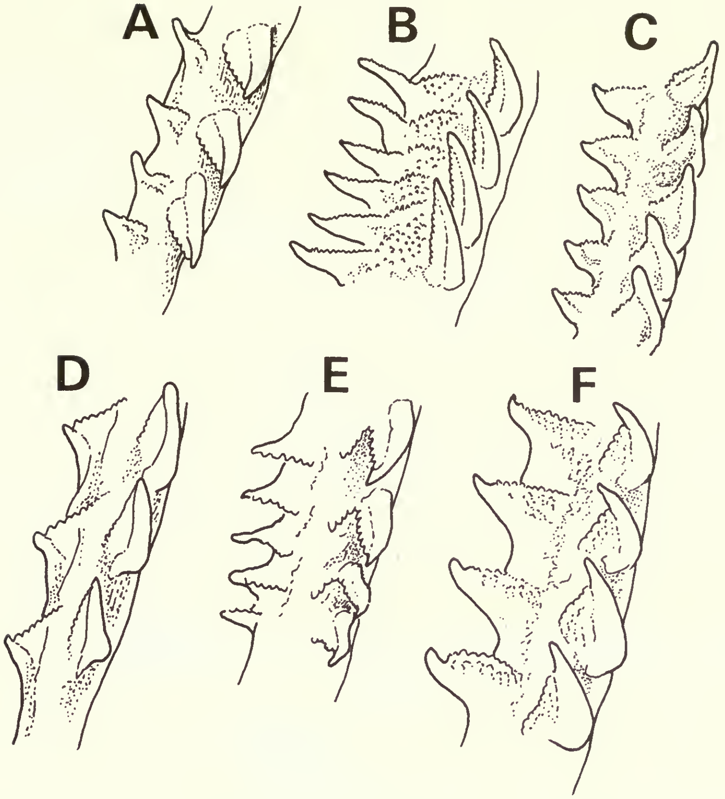

Fig. 5 Gill-raker morphology in A, *Genghis mongolicus*; B, *Oreoleuciscus humilis*; C, *Tribolodon brandti*; D. *Aspius aspius*; E, *Aspiopsis merzbacheri*; F, *Pogonichthys macrolepidotus*. All × 12, except B = × 25. A and E, left, others right 1st ceratobranchial.

Those features analysed above which serve to distinguish *'Leuciscus' mongolicus* from other *Leuciscus* species are specializations shared with genera of the *aspinine group* (see below, p. 291. *'Leuciscus' mongolicus* is, however, excluded from that group since it lacks the three synapomorphies defining it, namely, a high vertebral number, and numerous frontal, nasal sensory pores, and elongated pterosphenoid. As such it is necessary to assign *'Leuciscus' mongolicus* to a new genus:

GENGHIS gen. nov.

TYPE SPECIES. *Squalius mongolicus* Kessler, 1876. *In*: Prejevalsky, N. *Mongolia i strana Tangutov* **2** (4): 21, pl. II. Type locality, Dalai Nor.

ETYMOLOGY. After Genghis (Khan), below whose rampart lies the type locality, Lake Dalai.

DIAGNOSIS. Medium-sized cyprinid fish (the largest specimens measured, 225·5 mm SL), slender-bodied, distinguished from other non-barbelled cyprinids by a combination of the following features: somewhat humped nuchal profile; dorsal cranial profile gently sloped; mouth set obliquely at 45°; border of the 4th infraorbital attenuated and widely separated from the orbit; elongate pterosphenoid, laterally expanded and possessing a lateral shelf from which originates the *adductor arcus palatini* muscle; operculum with attenuated lower posterior border; gill-rakers spinous with crenate medial border; long gape between the branchial arch and pharyngo-buccal roof (Fig. 11); lateral line scales large; caudal fin deeply emarginate.

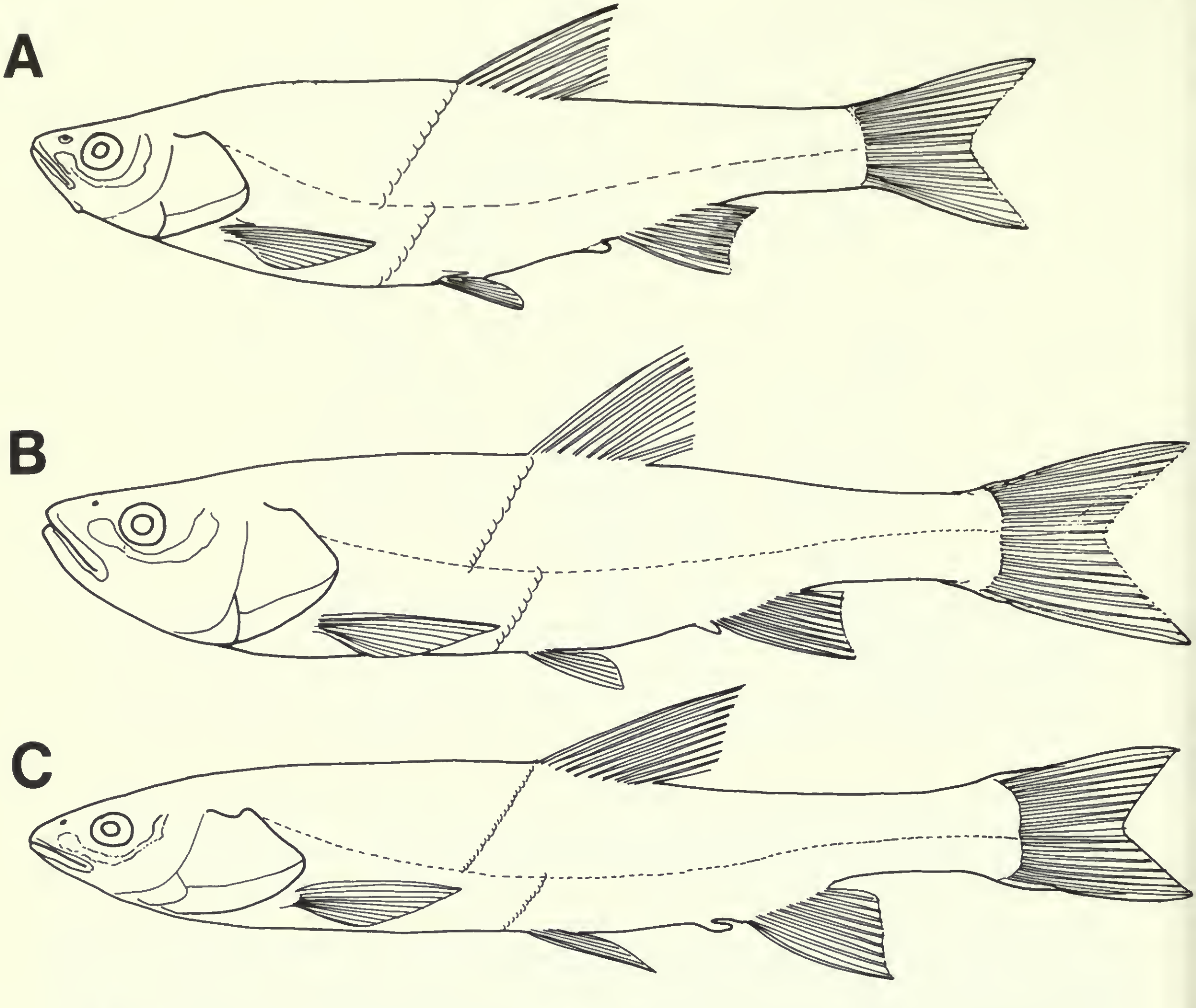

Fig. 6 Outline drawings of A, *Genghis mongolicus*; B, *Aspiopsis merzbacheri*; C, *Oreoleuciscus humilis.*

Genghis mongolicus (Kessler, 1876)

(Fig. 6A)

Squalius chinensis Prejevalski, 1876 *Mongolia i strana Tangutov* **1:** 135 *nomen nudum*
Squalius mongolicus Kessler, 1876. *In:* Prejevalsky, N. *Mongolia i strana Tangutov* **2** (4): 21, pl. II, fig. 2.
Squalius chaunchicus Kessler, 1876 *Ibid:* 23
Leuciscus farnumi Fowler, 1889 *Proc. Acad. nat. Sci. Philad.*: 179
Leuciscus mongolicus, Berg, 1912. *Fauna de la Russie* **3:** 92
?*Leuciscus mongolicus* Oshima, 1926 *Zoological Magazine* **38:** 100
Leuciscus (*Idus*) sp. Miyadi, 1940 *Fishes of Manchuria In:* Hydrobiological Investigations of Kwantung Province and Manchurian Empire: 41, fig. 30.
Leuciscus waleckii suiyuani Mori, 1941 *Zoological Magazine* **53** (3): 183, fig. 2.

NOTES ON SYNONMY *Squalius* Heckel, 1843 is a synonym of *Leuciscus* Cuvier, 1817. Berg (1912: 92 & 110) referred *Squalius mongolicus* Kessler to *Leuciscus* and considered *S. chaunchicus* Kessler a synonym, an opinion endorsed by Bănărescu (1970). Fowler (1899) described *Leuciscus farnumi* from three specimens, the holotype being from Lake Dalai. Fowler makes no mention of Kessler's species from that lake and his description is undoubtedly that of *mongolicus.*

Oshima (1926) described a new species named as *Leuciscus mongolicus* making no reference to the Kessler species which he had obviously overlooked. Oshima's species was later synonymized by Mori (1934) with *Leuciscus waleckii* (Dybowski, 1869). From Oshima's description it is difficult to tell if his species is Kessler's *mongolicus* or is Dybowski's *waleckii* as was assumed by Mori. Mori's concept of *Leuciscus waleckii* certainly appears to correspond with Dybowski's description of that species, and his illustration shows a fish that is clearly different from Kessler's *mongolicus.* Attempts to trace Mori's and Oshima's specimens have so far failed. Whether or not Oshima's *Leuciscus mongolicus* is synonymous with Kessler's *Squalius* (=*Leuciscus*) *mongolicus*, the fact remains that the name proposed by Oshima is a junior homonym for which I propose, as a *nomen novum, jeholi* as indicative of that species' locality.

Bănărescu (1970) recognized Mori's (1941) subspecies *L. waleckii suiyuani* as a synonym of *L. mongolicus*, an opinion with which I would concur. I can also confirm Bănărescu's (1970) opinion that *Leuciscus waleckii sinensis* Rendahl (1925) which also occurs in the Hwang-Ho drainage does indeed belong to that species complex. The possibility that Rendahl's subspecies might also be synonymous with Kessler's *L. mongolicus* has been dispelled by examination of the three syntypes which conform in every respect with Dybowski's *Leuciscus waleckii.*

DESCRIPTION. The following description amplifies that given under the generic diagnosis and is based on the following 18 specimens; AMNH 10907, 4 specs 138–146 mm SL; BMNH 1983.3.1:3–4, 2 specs 130·5; 147 mm SL (ex AMNH 10907); AMNH 10913, 7 specs 72–121 SL: AMNH 10908, 3 specs 93, 106, 145 mm SL; AMNH 10906, 2 specs 154, 222 5 mm SL. All from Paotow (Pao-t'ou), Suiyan Province, Inner Mongolia; collected by C. H. Pope.

As % of SL: body depth 20·1–27·7 (M25·5); head length, 26·2–29·2 (M26·2); caudal peduncle length, 15·9–21·9 (M18·3), caudal peduncle depth as % of its length, 49·2–63·9 (M58·0); as % of head length, interorbital width 24·5–32·0 (M28·8); snout length 21·3–29·6 (M25·7); eye diameter 17·8–23·6 (M22·1); opercular length 29·7–35·5 (M32·9).

Gill-rakers spinous, 3–4 on 1st epibranchial 18–10 on 1st ceratobranchial; extensive gap between branchial arch and bucco-pharyngeal roof (Fig. 12); pharyngeal bones slender, teeth biserial, slender, hooked numbering 5·3 (f3), 4·2 (f1), 4·3 (f2). Scales 9–10/50–52/7–8; Kessler gives a lateral line count of 54 and it is apparent from his figure that he was counting those pore-bearing scales extending onto the base of the caudal fin. Bănărescu (1970) gives a count of 52–54 for the type specimen of *G. mongolicus.* My counts are those of the standard length. Dorsal fin with III, 7 (f15), III, 8 (f3) rays; anal fin with III, 8 (f2) or III, 9 (f16) rays. Pectoral rays I, 16 (f13), I, 17 (f2), I, 18 (f2), I, 19 (f1); pelvic rays I, 8 (f9) I, 9 (f7).

Swimbladder is two-chambered, the posterior chamber reaching to above the genital opening. Genital papilla prominent with plicate margin. Small pectoral flap and an elongate pelvic axial scale present. Caudal fin emarginate, lobes pointed.

Distribution. The type locality is the lake Dalai (now Hu-lun Ch'ih) in the Nei Monggol, China, 48° N, 117° E; it lies in the plain between the Mongolian Plateau and the Ta Hsing-an-ling Shan-mo (Greater Khinghan) range. According to Berg (1949) there is no outflow of the lake. However, two main rivers flow into Dalai, that from the Mongolian Plateau is the Kerulen (Herlen or Ko lu-lun-Ho) and that from Lake Buyr in the Khingan mountains, is the Orxon (Wu-erh-Shun-Ho). The specimens examined are all from Paotow (Baotaou) on the Hwang-Ho river, some 88° south of the type locality.

Relationships of *Genghis* and the aspinines

The character analysis given above suggests that *Genghis* is closely related to the assemblage of five genera recognised by Howes (1978) as the *aspinine group*, viz.; *Luciobrama*, *Pseud-*

aspius, Aspiolucius, Aspius and *Elopichthys.* The derived characters uniting these genera are (1) posteriorly and laterally extended pterosphenoid, (2) elongation of posterior cranial bones with development of an occipital platform, (3) unique configuration of the infraorbitals, (4) high vertebral number, and (5) many nasal and frontal sensory pores.

Characters (1)–(3) are possessed by *Genghis* and have already been discussed; (4) and (5) are shared only amongst the *aspinine group* genera, and are discussed below.

Character (4). All aspinines have a total vertebral number in excess of 50 (51–55). Apart from *Pelecus,* with 52 and *Ochetobius* with 61, no other cyprinid has such a high vertebral count (see Howes, 1978). In the aspinines the increase is in the abdominal vertebrae. In three genera, however, namely *Aspius, Elopichthys* and *Aspiolucius,* there is a high number of caudal vertebrae, 22–24 cf. 21 in *Luciobrama* and *Pseudaspius*, a figure that compares with the modal number of other cyprinids viz. 24 (calculated in part from figures published in Howes, 1978, table 1, and from unpublished data). *Pelecus* and *Ochetobius* have both high abdominal and caudal counts. *Genghis* has a total of 45 vertebrae.

Character (5). Aspinine genera share a high number of nasal and frontal sensory pores, respectively 8–10 and 10–22. These counts are unusually high amongst cyprinids; in general the nasal is a short bone with 2–3 pores (exceptionally 6 in some cultrines) and the commonest number of frontal pores is 5–6. Some abramine taxa have 9–10 frontal pores (e.g. *Hypophthalmichthys,* see Howes, 1981 : 17), but the frontal morphology of the abramines and their recognition as monophyletic on the basis of other synapomorphies, suggests an independent derivation of increased sensory pore numbers. High numbers also occur in *Oreoleuciscus* (see below) and in species of the Nearctic genera *Ptychocheilus, Gila, Lavinia* and *Pogonichthys.* These genera, as is the case with aspinines, tend to have elongate crania and it may be that increased pore number is a straightforward correlation with cranial length. This does not always follow, however, since many cheline, bariliine, cultrine and schizothoracine taxa also have lengthened crania but show no sign of an increase in frontal pore number. By itself it would be dubious to treat a high frontal pore number as synapomorphic but in combination with increased numbers of nasal and mandibular pores it seems a valid synapomorphy for aspinine taxa. Whether this is also the case for the high frontal pore number in the Nearctic taxa demands further investigation.

A character overlooked by Howes (1978) when considering aspinine group synapomorphies is the extreme development of the coronomeckelian bone. The usual cyprinid condition is for the bone to be small and irregularly shaped, with a medial shelf on to which inserts the tendon of muscle A_2. Among the aspinines, the coronomeckelian bone of *Luciobrama* is the most derived, being a long, almost boomerang-shaped element with a wide medial shelf (Fig. 7C). In *Elopichthys* the coronomeckelian has an irregular shape but with a long anterior process. The shape of the bone in *Aspius* is most like that of *Genghis*, being broadly triangular with a wide medial shelf (Figs 7A & B). Departure from the general cyprinid condition also occurs in *Tribolodon, Oreoleuciscus, Pogonichthys* and *Ptychocheilus* where it is long and triangular (Figs 7D–F). A similarly shaped bone is present in some *Phoxinus* species. The value of this character is difficult to judge, as its development may be related to the insertion of the adductor muscle. From the various teleost jaws figured by Nelson (1973) it seems that there is much variability in the size of the coronomeckelian; in some plesiomorphic groups (e.g. gonorynchids, esocoids, amiids) the bone appears insignificant, whilst in others (hiodontids, albulids, argentinoids) it is extensive. All that can be said is that in aspinines and the other taxa considered above, the coronomeckelian is of a particularly unusual (and possibly derived) shape which may represent a synapomorphy.

The relationships of *Genghis* plus the aspinines must now be considered. Howes (1978) thought *Oreoleuciscus* (Fig. 6C) the most likely candidate as the sister group of the aspinines. It is now clear that this is not the case since *Oreoleuciscus* possesses none of those characters uniquely shared by *Genghis* and the *aspinine group.* Nonetheless, *Oreoleuciscus* has a close affinity with these taxa as it shares with them and with *Tribolodon* both an elongate pterosphenoid bearing a lateral shelf from which originates part of the *adductor arcus palatini* musculature, and crenate gill-rakers. The configuration of the infraorbitals in *Oreoleuciscus*

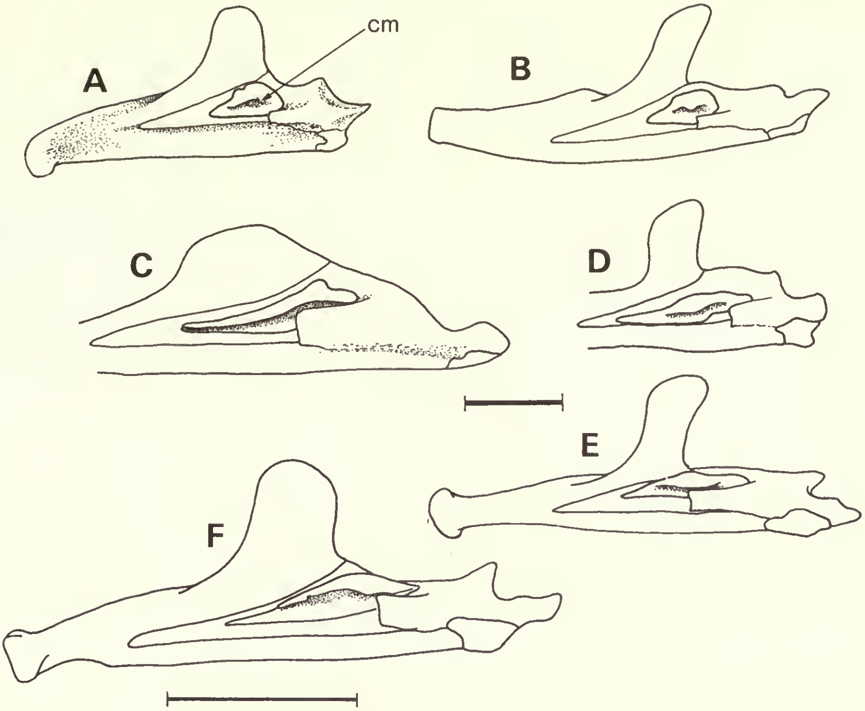

Fig. 7 Lower jaws, medial views to show coronomeckelian bone (cm) of, A, *Genghis mongolicus;* B, *Aspius vorax;* C, *Luciobrama macrocephalus;* D, *Oreoleuciscus humilis;* E, *Pogonichthys macroleptidotus*; F, *Tribolodon brandti.* Scales = 5 mm.

resembles that of the aspinines and *Genghis* in that the 3rd infraorbital extends, almost horizontally, well past the posterior border of the orbit with a consequent separation of the 4th infraorbital from the orbital margin. However, the 4th infraorbital is reduced to its canal tube and is not diagonally aligned, as in the aspinines and *Genghis* (cf. Figs 3A, C & D with fig. 22 in Howes, 1978).

A simple sister-group relationship between *Oreoleuciscus* and *Genghis* plus the aspinines is disrupted by the monotypic genus *Aspiopsis* (Fig. 6B). Only a single syntype is available for examination and only those characters visible without dissection and from radiographs can be ascertained. Howes (1978 : 60) followed Berg (1949) in considering *Aspiopsis* to be synonymous with *Leuciscus,* but a reappraisal of *Aspiopsis* makes it clear that it is a distinct genus and must be included amongst the assemblage of genera discussed here.

Aspiopsis is characterized by a rather elongate body, an operculum with attenuated posterior border, small, imbricate scales (70 in the lateral line), numerous gill-rakers (27 on the 1st ceratobranchial) with a crenate medial membrane, and a papillate lateral buccal membrane, particularly over the preopercular area adjacent to the gill-arch. Radiographs reveal an elongate cranium. In the shape and configuration of its infraorbitals, *Aspiopsis* closely resembles *Genghis* and the aspinine genera (Figs 3C). The 1st infraorbital, however, bears a V-shaped depression on its dorsal margin, a feature encountered elsewhere only in *Tribolodon.* In these characters, apart from the latter, *Aspiopsis* most clearly resembles *Oreoleuciscus.* Lack of dissectable material precludes investigating the site of origin of the *adductor arcus palatini* muscle in *Aspiopsis.* Assuming that this muscle does originate from the pterosphenoid, then *Aspiopsis* would be considered as the sister-lineage to *Oreoleuciscus.* On the basis of their cranial elongation *Aspiopsis* and *Oreoleuciscus* appear most closely related to *Genghis* and the aspinines; however, the derived 1st infraorbital morphology which

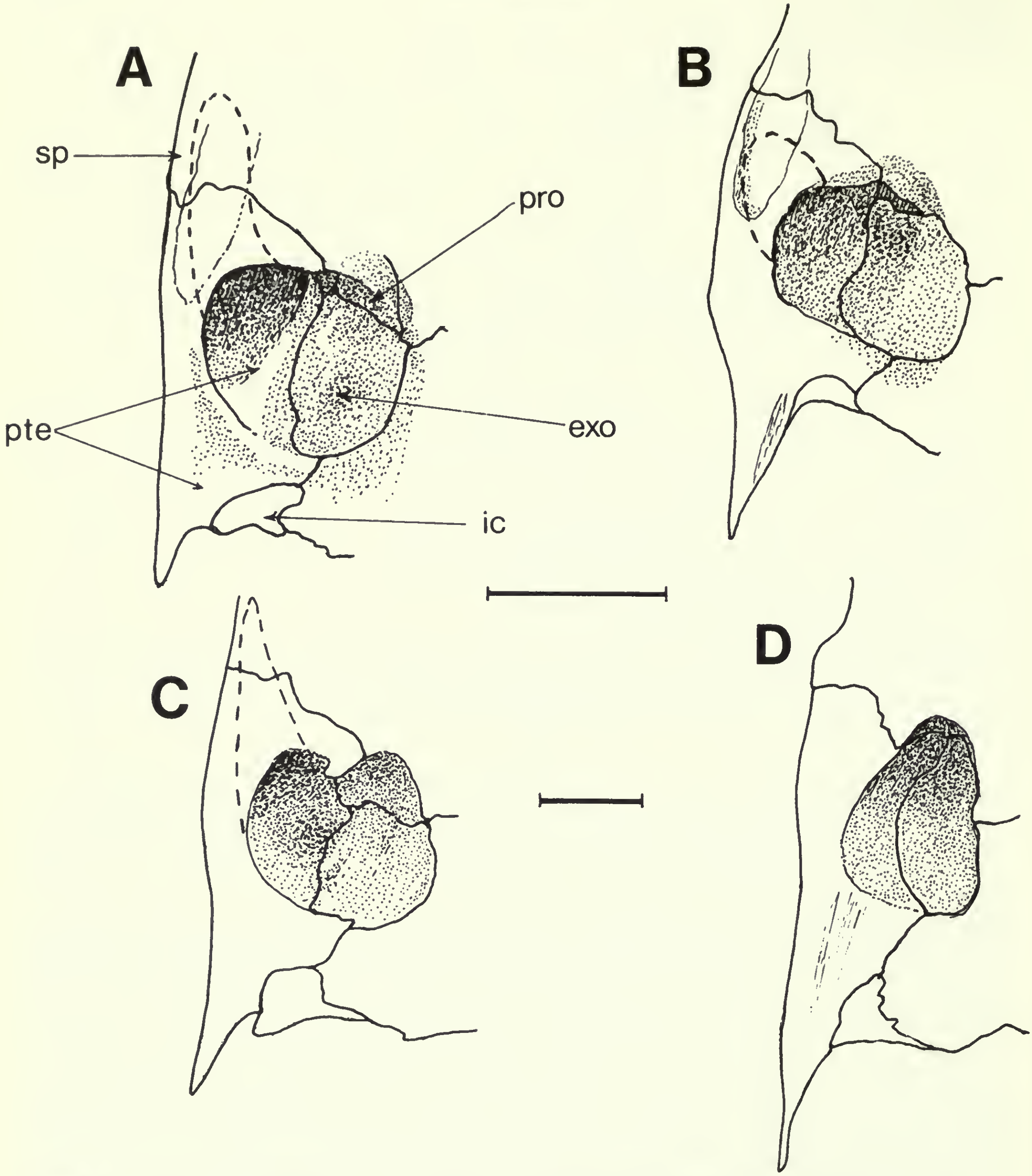

Fig. 8 Subtemporal fossae of A, *Tribolodon brandti;* B, *Ptychocheilus oregonensis;* C, *Pogonichthys macrolepidotus;* D, *Aspius vorax,* dashed lines indicate extent of the anterior chamber.

Aspiopsis shares with *Tribolodon* places the *Aspiopsis–Oreoleuciscus* lineage in an unresolved trichotomy, with *Genghis* and the aspinines on the one hand, and *Tribolodon* on the other. The trichotomy may be resolved when the anatomy of *Apsiopsis* is better known.

Tribolodon, as well as sharing a derived infraorbital feature with *Aspiopsis* also shares with the aspinines, *Genghis, Oreoleuciscus* and the Nearctic genus *Pogonichthys,* a pterosphenoid

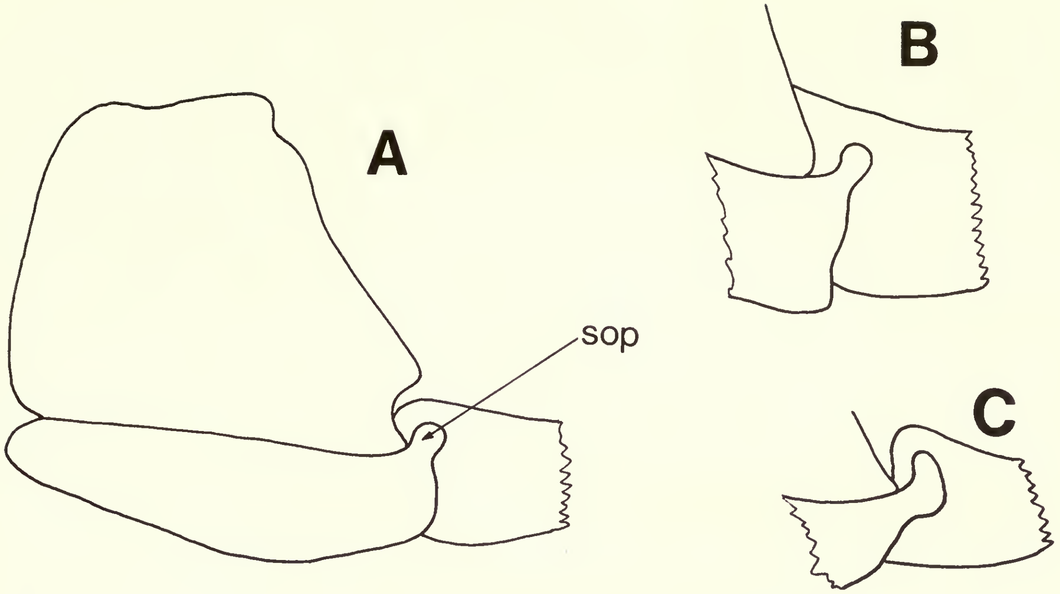

Fig. 9 Suboperculum, medial views showing anterior process (sop) of A, *Tribolodon brandti;* B, *Pogonichthys macrolepidotus* (210 mm SL); C, *Ptychocheilus grandis* (UMZM 181 929–5, 315 mm SL).

origin of the *adductor arcus palatini* muscle, crenate margined gill-rakers, and a triangular coronomeckelian bone. In addition, *Pogonichthys*, shares with *Tribolodon* a derived form of subtemporal fossa, suboperculum and caudal skeleton as follows:

The *subtemporal fossa* in *Tribolodon* and *Pogonichthys* has an anterior extension into the autopterotic and sphenotic (Fig. 8). The extension is in the form of a narrow, finger-shaped chamber filled with a plug of fat. A sphenotic contribution to the subtemporal fossa was recognized by Howes (1982) as a synapomorphic condition for an assemblage of barbelled carps, named the *squaliobarbine group.* In these taxa however, the subtemporal fossa has a different shape in that the fossa is more extensive, with the prootic and exoccipital contributing substantially to its roof. Furthermore, in the squaliobarbines, part of the *levator posterior* muscle originates from the sphenotic chamber. In *Tribolodon* and *Pogonichthys* the *levator posterior* takes its origin dorsally from the pterotic and epioccipital only, and posteriorly from the exoccipital—as in the case of *Cyprinus* shown by Eastman, 1971—, the sphenotic is not involved. This particular type of fat-filled sphenotic chamber in *Tribolodon* and *Pogonichthys* has not been discovered in any other cyprinid examined. In *Ptychocheilus,* there is a lateral cavity of the subtemporal fossa in the pterotic and this too contains a fatty plug (Fig. 8). Amongst the aspinine genera the subtemporal fossa is small and trianguloid in outline (Fig. 8).

The *suboperculum* in *Tribolodon* and *Pogonichthys* has a club-shaped antero-dorsal process (Figs 9A & B). Normally this part of the bone is rounded, or, if produced, it is in the form of a slender triangle. A similarly shaped subopercular process also occurs in *Ptychocheilus* (Fig. 9C).

The *caudal skeleton* in *Pogonichthys* and *Tribolodon* exhibits hypertrophy of the preural neural spines. In *Pogonichthys* the neural spines of the 2nd-4th preural centra are thickened and antero-posteriorly lengthened and articulate distally with hypertrophied procurrent rays (Fig. 10A). In *Tribolodon* the 2nd and 3rd preural neural spines bear prominent anterior lamellae (Fig. 10B). Cyprinids are generally conservative in the morphology of the caudal skeleton and hypertrophy of the preural neural spines is rare. Often, however, there is a

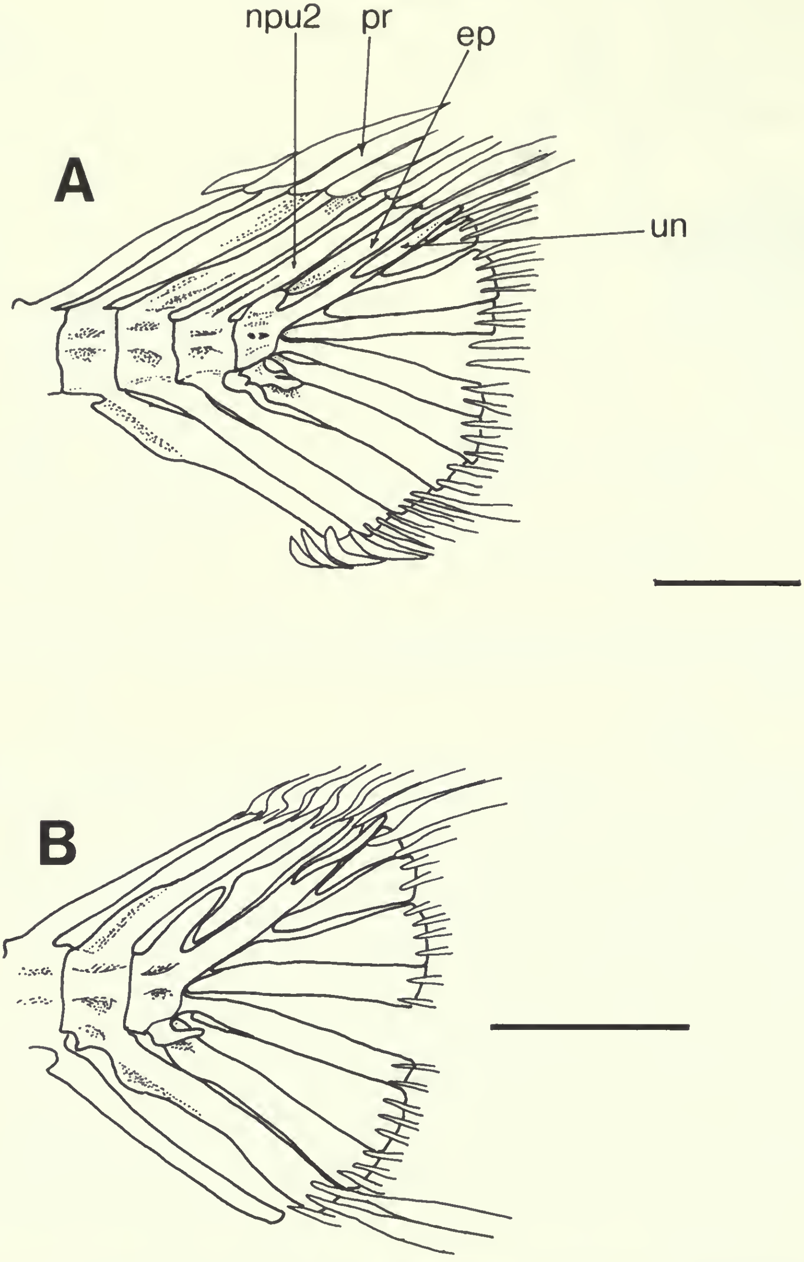

Fig. 10 Caudal skeletons of A, *Pogonichthys macrolepidotus;* B, *Tribolodon brandti;* ep = epural, pr = procurrent ray, npu2 = neural spine of 2nd preural vertebra, un = uroneural. Scales = 5 mm.

double neural spine on the 3rd preural centrum, and this feature regularly occurs among aspinine species. It is possible that the hypertrophied condition of the spines in *Tribolodon* and *Pogonichthys* is due to coalescence of the spines into a single unit. The Nearctic genera *Ptychocheilus* and *Lavinia* also display thickening of the preural neural spines and *Lavinia* has hypertrophied dorsal procurrent rays, a feature shared with *Pogonichthys.* There is further evidence to suggest *Pogonichthys* and *Ptychocheilus* have close phylogenetic links.

Ptychocheilus shares with *Tribolodon* and *Pogonichthys* the club-shaped subopercular anterior process (see above & Fig 9). *Ptychocheilus* also has crenate and papillate gill-rakers. In *Ptychocheilus oregonensis* the anterior fibres of the *adductor arcus palatini* muscle originate from the lower part of the pterosphenoid, but there is no prominent pterosphenoid shelf like that in *Pogonichthys.*

The cladistic relationships of the Nearctic 'aspinines' *Pogonichthys* and *Ptychocheilus* have yet to be ascertained. Apparent synapomorphies linking *Ptychocheilus* with the Nearctic genera *Mylopharodon* and *Gila* (part) have been reported. Hopkirk (1973) pointed out the similarity of jaw and gill-raker structure with *Mylopharodon* and Illick (1956) drew attention to the looped canal on the 1st infraorbital in both *Ptychocheilus* and *Gila robusta.* According to Illick (1956) this canal configuration does not exist in other Nearctic taxa and I have not found such an erratic course of the canal in any Old-World cyprinid taxon.

To summarize; *Genghis* represents the sister lineage of the aspinine genera, *Aspius, Elopichthys, Pseudaspius, Aspiolucius* and *Luciobrama,* which in turn from one part of a triad whose two other lineages are *Aspiopsis* + *Oreoleuciscus* and *Tribolodon* + *Pogonichthys.* It cannot as yet be determined which of these two lineages is the closest relative of *Genghis* and the aspinine group. This impasse is expressed as an unresolved trichotomy in the cladogram (Fig. 12).

Now that the *aspinine group sensu* Howes (1978) are seen to form one part of a more extended monophyletic assemblage, it is necessary to broaden the concept of the *aspinine group* so as to embrace *Genghis, Aspiopsis, Oreoleuciscus, Tribolodon* and *Pogonichthys.* The wider relationships of the aspinines are presently unclear. However, in discussing the characters which distinguish '*Leuciscus*' *mongolicus* from other *Leuciscus* species it was noted that two species, *L. lehmanni* and *L. schmidtii* possess a gill-raker morphology similar to that of *Genghis mongolicus.* Furthermore, these two species have an extensive gap between

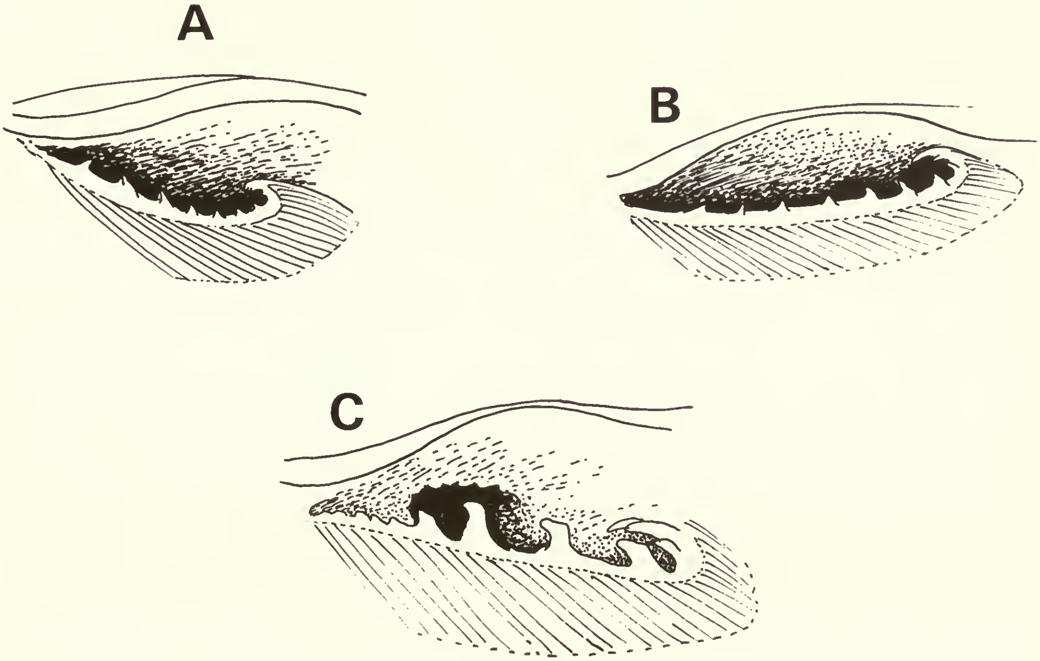

Fig. 11 Ventral view of 1st gill-arch (operculum raised) to show extensive opening between it and the bucco-pharyngeal roof in A, *Genghis mongolicus* and B, *Aspius aspius*, and the restricted opening in C, *Leuciscus leuciscus.*

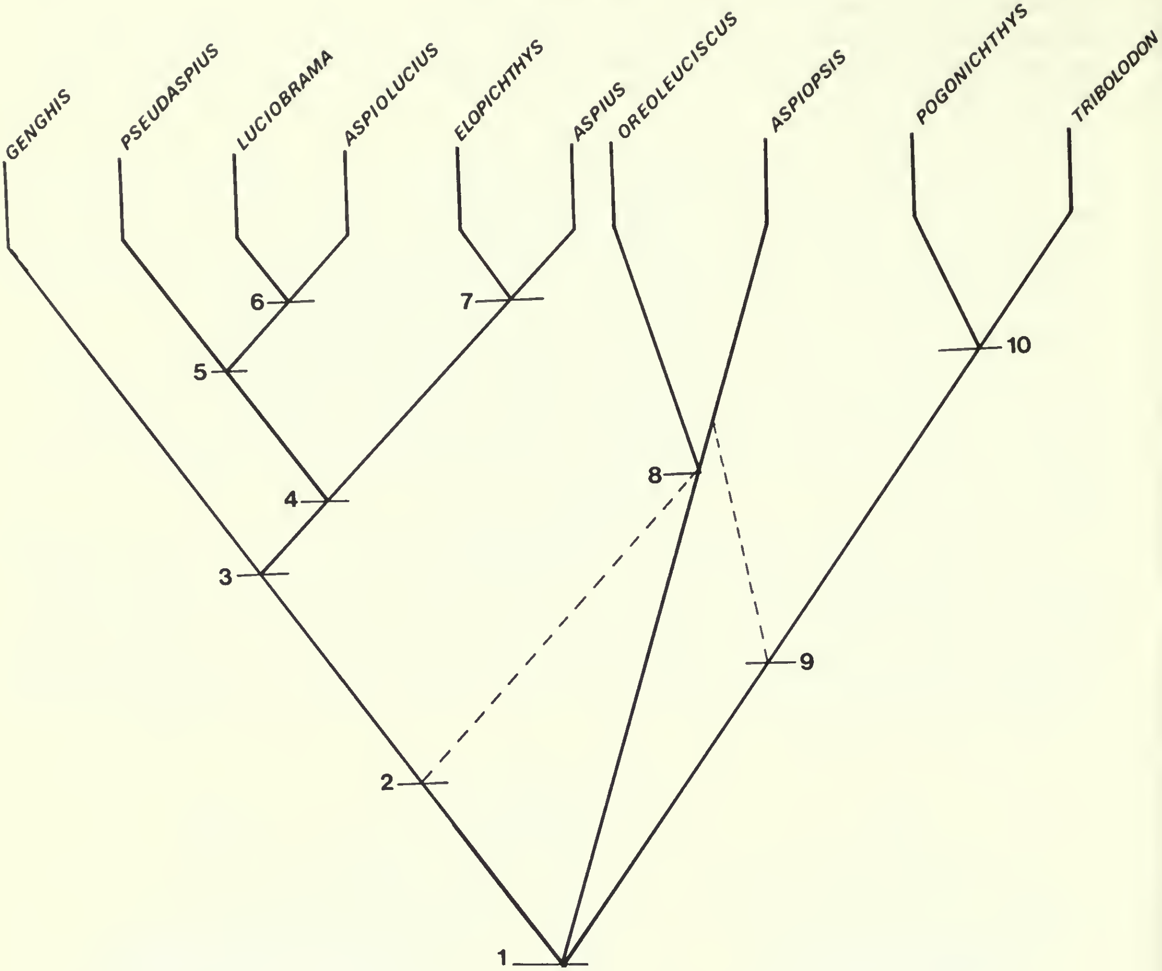

Fig. 12 Cladogram depicting the hypothesized relationships of the *aspinine group*. Synapomorphies: (1) Crenate margined gill-rakers; AAP muscle originates from pterosphenoid shelf; elongate, triangular coronomeckelian bone (this character of dubious polarity). (2) Derived infraorbital configuration; elongate posterior cranial bones. (3) Further derived state of infraorbital morphology; well-formed occipital platform; elongate and laterally expanded pterosphenoid. (4) Vertebrae 51–55; extensive contact between pterosphenoid and parasphenoid; nasals elongate with 6–10 pores. (5) Elongation of occipital region and lower jaw; tunnel-like post-temporal fossa. (6) Extreme divergence of 4th and 5th infraorbital canals; elongation of ento- and metapterygoid; complex development of LAP muscle. (7) Extensive aortic foramen in basioccipital process; 13–16 supraneurals. (8) Papillate lateral buccal membrane; attenuated operculum. (9) Concavity of 1st infraorbital (shared only with *Tribolodon*). (10) Club-shaped subopercular process; hypertrophy of preural neural spines.

the branchial arch and pharyngo-buccal roof, in contrast to the restricted space of other *Leuciscus* species (Table 1 & Fig. 11). It seems likely that '*Leuciscus' lehmanni* and '*L.' schmidtii* (both from Central Asia) may represent the sister group to the aspinines, and that the whole assemblage is the sister group to an, as yet, unidentified monophyletic unit within the all-embracing '*Leuciscus*'. These ideas can only be tested by a revision of '*Leuciscus*' (see comments below in Conclusion section).

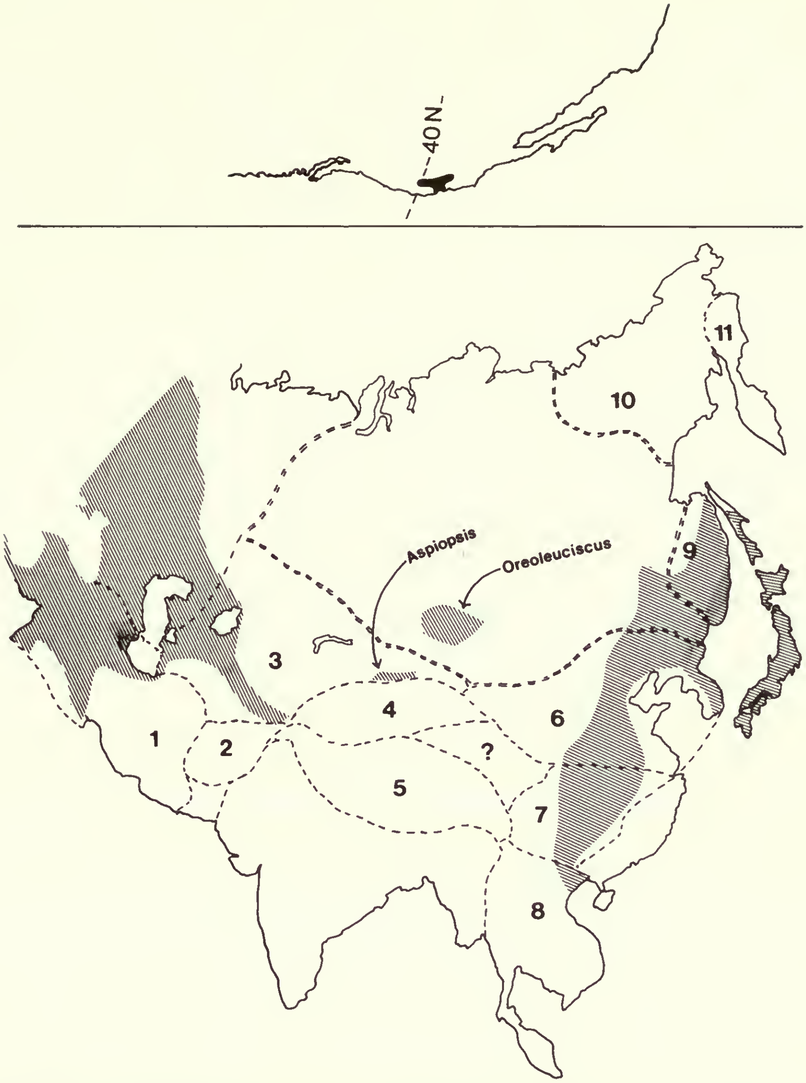

Fig. 13 Distribution of the *aspinine group* in Asia (hatched, below) and western North America (solid black, above). The numbered zones on the Asian map refer to the disposition of accreted continental plates as proposed by McElhinny *et al.* (1981) and Leith (1982). Double-dashed lines indicate the boundary of the Siberian craton. Plates; 1 = Iranian, 2 = Afghanistan, 3 = Kazakhstanian, 4 = Tarim, 5 = Qinhai-Tibet, 6 = Sino-Korean, 7 = Yangtze, 8 = SE Asian, 9 = Sikhote Alin, 10 = Kolyma, 11 = Kamchatka. Map of Asia drawn on Zenithal equal-area projection.

Biogeography of the aspinines

Distribution within Asia

The most significant feature of aspinine distribution within Asia is its east-west dichotomy (Fig. 13). *Aspius* lies to the west, covering much of Europe and extending south to the Tigris. *Aspiolucius* occurs sympatrically with *Aspius* in the Amu Darya (see Coad, 1981). The majority of aspinine genera are distributed east of the Mongolian plateau; *Elopichthys,* the

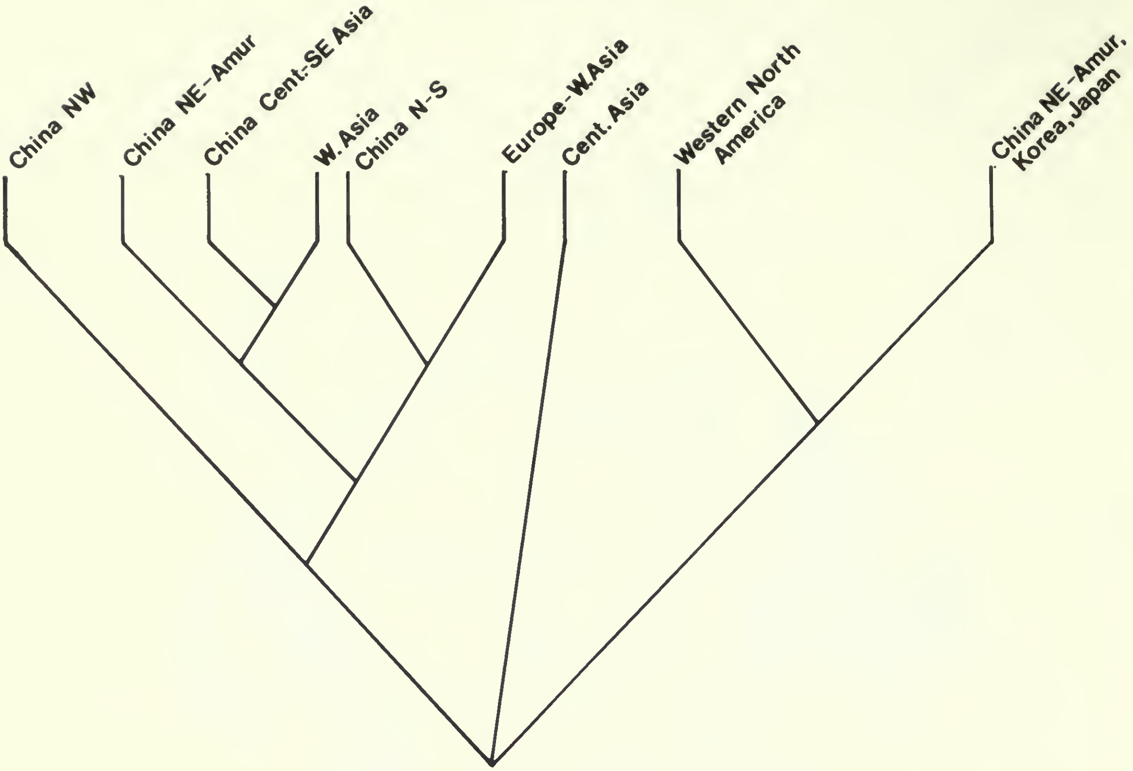

Fig. 14 Area cladogram of the aspinine group.

sister genus of *Aspius; Pseudaspius* and *Luciobrama*, the relatives of *Aspiolucius,* all lie in the Sino-Korean region (including the Amur; the Siberian and China subregions of Mori, 1936). *Luciobrama* extends south to Hanoi. The plesiomorphic aspinines, *Genghis* and *Tribolodon* also occur in eastern Asia. The former in northern China and the latter along the coastal margin of the Yellow Sea and the Sea of Japan and the Pacific coasts of Japan and Sakhalin. Only two genera, *Aspiopsis* and *Oreoleuciscus* occur in Central Asia, being confined, respectively to a small area bordering Sinkiang and the landlocked basins of the Upper Ob and Bya in Mongolia.

An area cladogram of the Asian aspinines shows a repeated dichotomy in the two lineages between western and eastern Asia (Fig. 14). The lineage of central Asian genera forms part of an unresolved trichotomy with the East Asian and Japanese–American branches and so is uninformative as to its area relationships.

Trans-Pacific links

The phyletic relationships established here between *Tribolodon* and *Pogonichthys* supports the hypotheses of Miller (1959; 1965), Hopkirk (1973), Gosline (1974) and Howes (1980) that a close relationship exists between some western North American and Japanese and Chinese cyprinid taxa. This Pacific link is the only one so far known for members of the Cyprinidae, although a well-known relationship exists elsewhere within cyprinoids, namely that between Chinese and American catostomids (see Patterson, 1981). The area cladograms presented by Patterson (1981) for various Nearctic and Palearctic freshwater teleosts, suggest closer links between western-North America and eastern America and Europe than with Asia.

Links between eastern Asia and western-North America are, however, forthcoming from cladistic relationships established amongst various insect groups. Ross (1974) demonstrates a Pacific link for caddisflies and Edmunds (1981) in discussing the distribution of mayflies points to the relationships between Eurasian and Nearctic genera as displaying strong Pacific vicariant patterns. Tuxen's (1977) analysis of proturans points out an 'unexplained' geographic relationship between Japanese and a Nearctic species of *Baculentulus.*

Explanations for an eastern Asia–western-North American faunal association may be attributed to dispersal or vicariance. At present too few phylogenetic data are available to discriminate between these alternative explanations. It has generally been accepted that the Bering land connection has been the principal route for faunal dispersal from late Cretaceous (see Cox, 1974 : 86 concerning 'Asiamerica'). More recent notions have proposed that several continental plates (or terranes) have occupied what is now the Pacific Ocean and that these elements are now accreted to the margins of the Asiatic and American cratons (see discussions in Nur & Ben-Avraham, 1981 and Jones *et al.,* 1982). Thus, Asia and North America are hybrid continents and from a vicariant point of view areas of related biotic endemism within those continents should mark former plates and their associations. The numbers of plates and their former dispositions, and whether or not there were supercontinents Gondwanaland and Pacifica are hotly disputed subjects amongst geologists (see McElhinny *et al.* 1981; Batten & Schweichert, 1981; Leith, 1982; Audley-Charles, 1983; Kerr, 1983).

The distributional pattern of the aspinines within Asia and between Asia and western-North America provides general support for a vicariant explanation involving continental plate displacements. However, only more congruent cladograms of east Asiatic and western-North American biota will favour such an explanation.

Conclusion

Further progress with understanding the relationships of leuciscine and aspinine cyprinid fishes depends on:

(1) A revision of *Leuciscus.* Such will not be an easy task since apart from the strictly practical problem concerned with lack of adequate samples of Russian and eastern Asian species in Western European museums, the would-be reviser faces the taxonomic problem of dealing with what is seemingly a plesiomorphic assemblage of species.

(2) Conduct a more wide-ranging cladistic analysis of Palearctic and Nearctic non-barbelled cyprinids.

(3) Consolidation of the trans-Pacific link hypothesis through a more wide-ranging vicariance analysis of other biotas.

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New bats (Mammalia: Chiroptera) and new records of bats from Borneo and Malaya

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Introduction

Although numerous bat species are known from Sabah, many records (Medway, 1977) originate in collections made from Mount Kinabalu or from the montane region of which it forms a part. Bats from the lowland areas of Sabah have received less attention and moreover many records are of cavernicolous species. One of us (CMF) has since 1981 been working as a Canadian volunteer (CUSO) for the Wildlife Branch of the Sabah Forest Department. While the principal activity in Sabah has been the management of edible-nest swiftlets (*Collocallia*) and the study of the rain forest avifauna, it has also been possible to capture and study bats, of which a proportion has been retained as museum specimens for taxonomic and record purposes. Some 65 species have been obtained, including three hitherto undescribed, some, including a new subspecies, representing new distributional records for Borneo, and others of taxonomic or more local distributional interest. This account is limited to the novelties that have been obtained, to those specimens that constitute new records for Borneo, and those that represent taxa so far poorly known. A single new record for Malaya has also been included.

The majority of the bats were caught using harp-style traps (Tuttle, 1974; Tidemann & Woodside, 1978). Usually these were placed across narrow trails or streams in the rain forest, or near cave openings. Some bats were also caught in standing mist nets, others by hand or with a butterfly net at their roosts in caves. All trapping has been done at or near ground level, with no work being attempted in the canopy.

Most of the collecting has been carried out either at Gomantong or Sepilok. The first of these, several miles north of the Kinabatangan River, about 20 miles south of Sandakan, has a network of limestone caves surrounded by both primary and secondary forest. Large colonies of several species of bats roost in the caves, while many other species are found in the vicinity. Bats from the Gomantong Caves were collected in 1929 by F. N. Chasen, and in 1930 by Senior Forest Ranger P. Orolfo (Chasen, 1931). More recently, Gomantong has been visited by the members of a Japanese group, in 1976 and 1979, the bats collected being reported by Kobayashi *et al.* (1980). These workers also obtained bats at the Madai Caves, whence some of those reported here originate. Sepilok is a virgin jungle reserve located near Sandakan and maintained by the Sabah Forest Department as a research area and wildlife sanctuary. Limited collecting has also been carried out at other sites which are summarized in Table 1.

Many of the more interesting specimens have been donated to the British Museum (Natural History), as have the holotypes of the new taxa described in this paper. All are denoted by their accession numbers, prefixed BM(NH). The final disposition of the remainder of the specimens examined in London has yet to be decided: all are indicated in this account by their original collector's numbers, prefixed CMF. Duplicates of some of these, together with those specimens that were not sent or brought to London since they represent

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Table 1 Major localities whence bats have been obtained

Gomantong	5°31′N, 118°04′E.	30 m	Limestone caves, in primary dipterocarp forest
Baturong	4°42′N, 118°00′E.	80 m	Limestone caves, in primary dipterocarp forest
Madai	4°43′N, 118°09′E.	80 m	Limestone caves, in logged dipterocarp forest
Panggi	5°31′N, 118°18′E.	150 m	Limestone caves, in logged dipterocarp forest
Segarong	4°34′N, 118°25′E.	30 m	Limestone caves near the sea, in secondary forest and mangrove
Sepilok	5°52′N, 117°56′E.	30 m	Primary dipterocarp forest
Lumerau	5°12′N, 118°52′E.	40 m	Primary dipterocarp forest
Sungei Labau, Witti Range	5°16′N, 116°30′E.	300 m	Primary dipterocarp forest
Silabukan	5°11′N, 118°47′E.	300 m	Primary dipterocarp forest
Rinangisan, Crocker Range	c. 5°40′N, 116°20′E.	110 m	Montane forest
Kinabalu National Park	6°02′N, 116°32′E.	1500 m	Montane forest
Menggadong	4°58′N, 115°28′E.	30 m	Kerangas Forest

species already well known in Borneo or of common occurrence will be maintained as a reference collection at Sepilok by the Sabah Forest Department.

All measurements are in millimetres: those of individual teeth have been made with a stereoscopic microscope and traversing micrometer stage, others with a dial micrometer.

Systematic section

Rousettus spinalatus Bergmans & Hill, 1980

Rousettus spinalatus Bergmans & Hill, 1980 : 95. In or near Medan, or in or near Prapat, N Sumatra.

SPECIMEN EXAMINED. ♂ CMF 0100 Panggi, Sabah (in alcohol, skull extracted).

REMARKS. This is the second example of *Rousettus spinalatus* to be recorded from Borneo, the first being a subadult female obtained at Niah Great Cave in Sarawak and reported by Bergmans & Hill in the original account. As in the original specimens, the wings in this example from Sabah are inserted on the spinal line and there is no longitudinal dorsal band of fur down the centre of the back. Dentally this specimen agrees closely with the example from Niah, although in the Sabah specimen, as in that from Niah, m^1 is slightly wider than the corresponding tooth in *R. amplexicaudatus*, not narrower as it is said to be in the original description. As in the Niah example, m^2 and m_3 are longer, wider and more massive than in *R. amplexicaudatus,* and m^2 is approximated more closely to the rear edge of the palate at the zygomatic insertion than in that species. A specimen (♀ CMF 0109) of *R. amplexicaudatus* was collected at Panggi on the day following that on which this example of *R. spinalatus* was obtained.

Measurements: length of forearm 86·9; thumb (c.u.) 25·3; II^m 33·4; II^1 7·1; II^2 5·4; III^m 50·6; III^1 31·7; III^2 41·4; IV^m 49·2; IV^1 24·0; IV^2 28·4; v^m 47·7; V^1 22·4; V^2 26·4; length of ear 17·6; length of tibia 33·3; length of foot (c.u.) 17·9; greatest length of skull 34·9; condylobasal length 32·8; condylocanine length 31·7; rostral length (front of orbit to prosthion) 12·0; rostral length (front of orbit to tip of nasals) 11·4; palatal length 17·5; palatilar length 16·8; length palation—incisive foramina 16·0; length palation—basion 13·0; lachrymal width 10·0; least interorbital width 8·1; least postorbital width 7·8; zygomatic width 22·2; width of braincase 14·8; mastoid width 13·8; orbital diameter 8·6; c^1–c^1 (crowns) 6·7, (alveoli) 6·4; c^1–c^1 (internally, cingula) 3·8; pm^4–pm^4 (internally) 5·1; m^2–m^2 (crowns)

10·5; (alveoli) 10·4; width of mesopterygoid fossa 4·5; c–m^2 (crowns) 12·9, (alveoli) 12·7; length of complete mandible from condyles 25·6; length right ramus from condyle 27·1; mandibular height (angular process to tip of coronoid process) 11·5; c–m_3 (crowns) 14·3, (alveoli) 14·2. Length/width of cheekteeth: pm^3 2·19/1·31; pm^4 2·33/1·89; m^1 2·82/2·07; m^2 2·04/1·54; pm_1 1·19/1·28; pm_3 2·16/1·25; pm_4 2·38/1·62; m_1 2·51/1·56; m_2 2·21/1·61; m_3 1·63/1·20.

Chironax melanocephalus (Temminck, 1825)

Pteropus melanocephalus Temminck, 1825 : 190, pls 12, 16, figs 3, 4. Bantam, Java.

SPECIMEN EXAMINED. ♀ CMF 830105.1 Sepilok, Sabah (in alcohol, skull extracted).

REMARKS. *Chironax melanocephalus* has not before been reported from Borneo although known from southern Thailand, Malaya, Sumatra, Nias Island, Java and Sulawesi. The species was reviewed in some detail by Hill (1983) who reported further specimens from Sumatra, Java and Sulawesi and provided comparative notes.

This specimen agrees with those from the mainland, from Sumatra and from Java in the presence of a small antero-external supplementary cusp on the second upper premolar (pm^3) rather than with Sulawesian examples from which this cusp is absent. In most points of wing structure it is similar to specimens from the Malay Peninsula, Sumatra and Sulawesi, conforming to these in the relative lengths of the third, fourth and fifth metacarpals rather than with Javan examples in which these digital components are relatively slightly shorter, the third metacarpal especially so. The second phalanges of the fourth and fifth digits, however, are relatively a little shorter than those in most specimens from the mainland and from Sumatra, in this respect approaching or agreeing with specimens from Java and Sulawesi.

This female specimen has diffuse pale orange neck tufts (from specimen in alcohol): otherwise dorsally the pale based pelage is tipped with dark brown except on the head where the pelage is blackish, while ventrally it is pale greyish brown, becoming buffy on the throat and flanks.

Measurements (wing indices in parentheses): length of forearm 45·6 (1000); III^m 31·6 (693); III^1 22·4 (491); III^2 28·4 (622); IV^m 30·5 (669); IV^1 16·9 (371); IV^2 16·7 (366); V^m 30·2 (662); V^1 14·8 (325); V^2 15·5 (340); greatest length of skull 22·7; condylobasal length 22·0; condylocanine length 21·0; length front of orbit–tip of nasals 5·4; length orbit–nares 5·0; length orbit–gnathion 6·9; palatal length 11·6; length palation–incisive foramina 9·8; length palation–basion 8·6; lachrymal width 6·1; least interorbital width 4·4: least postorbital width 5·1; zygomatic width –––; width of braincase 9·8; mastoid width 10·6; orbital diameter 5·8; c^1–c^1 (crowns) 4·5, (alveoli) 4·2; (cingula, internally) 2·1; pm^4–pm^4 (crowns) 6·7, (alveoli) 6·2, (internally) 4·0; m^1–m^1 (crowns) 6·4. (alveoli) 6·0; width mesopterygoid fossa 3·1; c–m^1 (crowns) 7·3; length complete mandible from condyles 15·7; length right ramus from condyle 16·6; coronoid height 8·5; c–m_2 (crowns) 8·2.

Hipposideros bicolor bicolor (Temminck, 1834)

Rhinolophus bicolor Temminck, 1834 : 19, pl. 1, fig. 3; 1835 : 18 (further description). Anjer coast, northwestern Java (Tate, 1941).

SPECIMENS EXAMINED. ♂♂ BM(NH) 83.66, 83.340 (in alcohol, skulls extracted), ♀ CMF 821212.2 (in alcohol) Gomantong, Sabah; imm. ♀ BM(NH) 83.339 Panggi, Sabah (in alcohol).

REMARKS. Peters (1869) listed *Hipposideros bicolor* from Sarawak but according to Medway (1977) the records of this species from central Borneo by Jentink (1897) are based on specimens of *H. dyacorum*. The adults of these from Sabah agree closely in size with one of *H. bicolor* from Java reported by Hill (1983) and are thus referred to the nominate subspecies rather than to *H. b. atrox* Andersen, 1918 which has a slightly smaller skull (condylocanine length (7) 15·4–15·9), although the differences are slight. This subspecies extends through the Malay Peninsula to the islands of Terutau, Tioman and Sumatra. Bornean specimens are considerably larger externally and cranially than *H. b. erigens* Lawrence, 1939 from the Philippine Islands.

Measurements (BM(NH) 83.66, 83.340, CMF 821212.2, in that order, cranial dimensions of 83.66 and 83.340): length of forearm 46·8, 45·5, 46·7; length of ear 16·7, 17·0, 17·5; length of tail 31·8, 29·9, 28·6; length of tibia 20·5, 19·5, 20·4; length of foot (c.u.) 8·0, 8·1, 8·3; greatest length of skull 18·9, 19·0; condylobasal length 16·6, 16·7; condylocanine length 16·4, 16·4; basal length 14·7, 14·8; palatal length 6·6, 6·6; width across rostral swellings 4·6, 4·5; least interorbital width 2·7, 2·7; zygomatic width 9·1, 9·2; width of braincase 8·5, 8·5; mastoid width 9·2, 9·5; c^1–c^1 (alveoli) 3·9, 3·9; m^3–m^3 6·0, 6·1; c–m^3 6·3, 6·5; m^{1-3} 3·9, 4·0; length complete mandible from condyles 11·4, 11·4; length right ramus from condyle 11·9, 12·0; c–m_3 6·8, 6·9.

Hipposideros ater Templeton, 1848

Hipposideros ater Templeton, 1848 : 252. Colombo, Sri Lanka.

SPECIMENS EXAMINED. ♂♂ BM(NH) 83.67—69 Gomantong (in alcohol, skulls extracted; ♂ CMF 821105.13 Madai (in alcohol).

REMARKS. There is no previous record of *Hipposideros ater* from Borneo although the species extends from India though southeastern Asia to Australia. It is difficult to allocate these specimens to subspecies since although in several points of size they agree closely with *H. a. saevus* Andersen, 1918 (S. Thailand to the Molucca Islands) or with *H. a. antricola* (Peters, 1861) (Philippine Islands) the sole complete skull is a little longer than in either of these. The anterior lower premolar (pm$_2$) is rather less than one half the length of the second lower premolar (pm$_4$) and about one half its height, as in *H. a. ater* from India and Sri Lanka or in *H. a. antricola* in which this tooth is also considerably reduced. For the present, therefore, specimens from Sabah are left unallocated: few examples are available for comparison and there are few published measurements of *H. a. antricola.*

Measurements (BM(NH) 83.67—69 in that order, forearm only of CMF 821105.13): length of forearm 40·4, 40·8, 40·7, 40·5; condylocanine length 15·3, ——, ——; width across rostral swellings 4·2, 4·3, 4·3; least interorbital width 2·7, 2·8, 2·9; zygomatic width 8·4, 8·3, ——; width of braincase 7·7, ——, ——; mastoid width 8·3, ——, ——; c^1–c^1 (alveoli) 3·5, 3·3, 3·6; m^3–m^3 5·6, 5·5, 5·7; c–m^3 5·6, 5·7, 5·7; length complete mandible from condyles 10·2, ——, 10·2; length right ramus from condyle 10·7, 10·5, 10·7; c–m_3 5·9, 6·0, 6·0.

Hipposideros cineraceus Blyth, 1853

Hipposideros cineraceus Blyth, 1853 : 410. Near Pind Dádan Khan, Salt Range, Punjab, India.
Phyllorhina micropus Peters, 1872: 256. Dehra Dun, near Simla, NW India.
? *Hipposideros wrighti* Taylor, 1934 : 237. Baguio, Benguet (near Headquarters gold mine), Luzon Island, Philippine Islands.

SPECIMENS EXAMINED. 2♂♂. 2♀♀ BM(NH) 83.341–344 Segarong, Sabah (in alcohol, skulls extracted); ♀ CMF 830221.2 Baturong, Sabah (in alcohol).

REMARKS. Andersen (1918) first listed Borneo within the distribution of *Hipposideros cineraceus,* probably on account of BM(NH) 10.4.5.160 from Banjermasin. More recently, Phillips (1967) has reported *H. c. cineraceus* from tidal caves in Sabah, at Tanjong Perawan, 4 miles north of the Bengkoka River, and at Tanjong Berungus, farther northward from the same river.

The species ranges from Pakistan eastwards through Indochina and Malaya to Borneo but has not been recorded from Sumatra or from Java. There is some variation in size (Table 2) over this extensive distribution, those from Borneo having forearms generally longer than those from Pakistan, India and Burma: those from Thailand and Malaya are to some extent intermediate in this respect. Bornean specimens average slightly larger in skull size than examples from the mainland but the difference is small. Specimens reported by Phillips (1967) agree in size with those recorded here: the measurement of the maxillary toothrow by this author appears to have been taken at the alveoli.

Table 2 Measurements of *Hipposideros cineraceus*

	Length of forearm	Condylocanine length	m^3–m^3	c–m^3
Pakistan, India, Burma	(21) 32·3–36·1	(16) 12·7–13·7	(19) 4·7–5·1	(19) 4·8–5·2
Thailand, Malaya	(23) 34·4–38·9	(7) 12·8–13·4	(11) 4·8–5·2	(12) 4·8–5·4
Borneo	(7) 34·0–39·6	(6) 13·2–13·8	(6) 5·0–5·4	(6) 5·2–5·5
Borneo (Phillips, 1967)	(4) 36·5–38·5	(2) 13·8–13·9		(3) 5·0–5·2
BM(NH) 79.11.21.160 Holotype of *micropus* Peters, 1872	36·0	12·6	4·6	4·9

Discussion. Specimens from northern India suggest that *Phyllorhina micropus* Peters, 1872 cannot be maintained as a distinct subspecies. The taxonomic history of *Hipposideros wrighti* Taylor, 1934 from the Philippine Islands was summarized by Lawrence (1939), who concluded that Taylor might have re-described *H. ater antricola* (Peters, 1861), having wrongly assumed that *antricola* referred to a bat of the longer-eared species now called *H. bicolor*, represented in the Philippines by *H. b. erigens* Lawrence, 1939. Hill (1963) followed this lead in synonymizing *wrighti* with *H. ater antricola*. However, further study of the original description of *wrighti* suggests that in fact it may more properly represent *H. cineraceus*, having a relatively long forearm (39) and small skull (condylobasal length 13·3, rostral width 4, zygomatic width 7, c–m^3 5·3, c–m_3 5·5, length of mandible 10) that agree more nearly with the dimensions of this species rather than with *H. ater*. This contention is supported by the account of the internarial septum, which is said to be 'folded and inflated, bulbous posteriorly, separated from lateral wings by deep grooves', although in *H. ater* the internarial septum is sometimes slightly inflated and swollen. If this suggestion is correct, the distribution of *H. cineraceus* must be extended to include the Philippine Islands.

Hipposideros ridleyi Robinson & Kloss, 1911

Hipposideros ridleyi Robinson & Kloss, 1911 : 241. Botanic Gardens, Singapore.

Specimens examined. ♀ CMF 821012.1 Sepilok, Sabah (in alcohol); ♂ CMF 830716.1 Menggadong, Sabah (in alcohol; coll. F. H. Sheldon).

Remarks. This species was first recorded from Borneo by Hill (1983) who reported a single specimen from Sepilok, Sabah. Length of forearm in this further example from that locality 47·8, in the specimen from Menggadong 47·6.

Myotis montivagus borneoensis subsp. nov.

Holotype Ad. ♀ BM(NH) 83.349 Sepilok, Sabah, 5°52′ N, 117°56′ E. Collected 10 April 1983 by C. M. Francis. Orginal number CMF 830410.9. In alcohol, skull extracted.

Other material. ♂♂ BM(NH) 83.345, 83.350, ♀♀ 83.74, 83.346–348. All from type locality (in alcohol, skulls extracted).

Diagnosis. Similar in most respects to *Myotis montivagus peytoni* Wroughton & Ryley, 1913 from northeastern India but with shorter forearm and larger skull; external size nearer to *M. m. federatus* Thomas, 1916 from Malaya but skull larger; considerably larger cranially than *M. m. montivagus* (Dobson, 1874) from Yunnan and Burma; differing from all of these in a greater degree of reduction of the canines, especially of c_1, which is about the same height as the last lower premolar (pm_4) rather than slightly higher.

Description. Ear long, narrow, its anterior margin convex, terminating basally in a subsquare insertion on the head, the tip rounded, the posterior margin straight for its distal half to a broadly angular emargination, then proximally convex, a moderate rounded lobe at the base, immediately above its insertion on the head. Tragus about as long as one half the length of the ear, its tip anteriorly directed, the anterior margin slightly concave, the posterior margin convex, slightly serrate for much of its length, with a well developed triangular lobe at its base. Wing inserted at base of first toe; calcar extending rather more than halfway to tail. Pelage thick and dense, rather long. Dorsal surface (from specimens in alcohol) blackish brown, the hairs blackish brown at the base and for much of their length, tipped with dark brown or chocolate brown, the tips faintly lustrous; ventral pelage similarly blackish brown at the base, tipped profusely with paler buffy brown.

Skull broad, not especially elongate, with broad braincase, low sagittal crest, wide interorbital region and widely flared zygomata; rostrum low and broad, in profile concave at frontal region, the anteorbital foramen separated from the orbit by a wide bar of bone; shallow frontal depression; narial emargination narrow, rounded, extending posteriorly about halfway to anteorbital foramina; palate wide posteriorly, with narrow anterior emargination extending posteriorly almost to a line joining the rear faces of c^1–c^1; short bony post-palatal extension; shallow, rounded basioccipital pits.

Inner upper incisor (i^2) small, bicuspid, rounded, with larger anterior cusp and smaller posterior cusp; outer upper incisor (i^3) short and wide, about twice bulk of inner tooth, with large central cusp flanked by small lateral cusps; anterior upper premolar (pm^2) small, about equal to i^3 in bulk, in contact with c^1 and posterior upper premolar (pm^4); second upper premolar (pm^3) minute, recessed between inner face of pm^2 and antero-internal face of pm^4, intruded from row; m^3 with three well developed commissures; lower incisors strongly arched forward, the first and second (i_{1-2}) small, tricuspid, third (i_3) at least twice the bulk of i_2 with irregularly cuspidate crown; c_1 small, about as high as the posterior lower premolar (pm_4) or slightly shorter; anterior lower premolar (pm_2) about one and one half times the bulk of i_3; second lower premolar (pm_3) minute, almost wholly intruded from row, partially recessed between postero-internal face of pm_2 and antero-internal face of pm_4.

Measurements appear in Table 3.

ETYMOLOGY. The subspecific name alludes to the provenance of this new subspecies.

REMARKS. Hill (1962) discussed the status of *M. montivagus* in some detail, giving measurements of specimens in the British Museum (Natural History) and associating *peytoni* and *federatus* with *montivagus*. This new subspecies from Borneo differs principally from the three mainland forms in greater cranial size, being especially larger than the nominate subspecies from Yunnan and Burma. Reduction and displacement of the second lower premolar (pm_3) varies within the species. In *M. m. montivagus* pm_3 is in the toothrow although compressed tightly between pm_2 and pm_4; in *M. m. peytoni* pm_3 may be in the row or partially intruded from it, while in *M. m. federatus* and *M. m. borneoensis* the tooth is almost wholly intruded from the row.

Myotis ridleyi (Thomas, 1898)

Pipistrellus ridleyi Thomas, 1898 : 361. Selangor, Malaya.

SPECIMENS EXAMINED. ♂, ♀ (BM(NH) 82.553–554 Sungei Labau, Witti Range, Sabah, 300 m (in alcohol, skull of 83.553 extracted); ♂ BM(NH) 83.75, ♀ CMF 821201.1 Sepilok, Sabah (in alcohol, skulls extracted).

REMARKS. Definitive records of this species have been confined hitherto only to Malaya, but it probably occurs also in Sumatra (Hill, 1969; Hill & Topal, 1973). These examples from Borneo are closely similar to Malayan specimens in the British Museum (Natural History).

External measurements (BM(NH) 82.553–554, 83.75, CMF 821201.1, in that order): length of forearm 28·4, 31·1, 28·8, 29·1; length of ear 11·2, 11·6, 11·1, 11·3. *Cranial measurements* (BM(NH) 82.553, 83·75, CMF 821201.1, in that order): greatest length of skull 11·8, 12·1, 12·2; condylobasal length 11·4, 11·6, 11·6; condylocanine length 10·8, 11·0, 11·0; width across anteorbital foramina 3·5, 3·4, 3·5; zygomatic width ——, 7·8, 7·9; least interorbital width 3·0, 2·9, 3·0; width of braincase 6·0, 5·9, 5·8; mastoid

Table 3 Measurements of *Myotis montivagus*

	M. m. borneoensis ♀ BM(NH) 83.349 Holotype	*M. m. borneoensis* Sabah	*M. m. peytoni* NE India	*M. m. federatus* ♀ BM(NH) 16.4.20.5 Holotype. Malaya	*M. m. montivagus* Yunnan, Burma
Length of forearm	42·2	(7) 42·2–44·8	(7) 45·0–47·0	39·0	(3) 40·0–41·5
Length of ear	15·1	(7) 15·1–16·1	(7) 15·0–15·5	—	(3) 8·5–14·5
Greatest length of skull	17·4	(7) 17·2–17·6	(7) 16·5–16·9	16·4	(2) 15·2, 15·4
Condylobasal length	16·5	(7) 16·4–16·9	(6) 15·9–16·3	15·7	(2) 14·7, 14·8
Condylocanine length	15·7	(7) 15·6–16·3	(6) 15·1–15·6	15·0	(2) 14·0, 14·1
Length anteorbital foramen–orbital rim	1·4	(7) 1·2–1·5	(7) 1·3–1·5	1·3	(3) 1·1–1·5
Least interorbital width	4·0	(7) 3·9–4·1	(7) 3·7–4·1	3·9	(2) 3·6, 3·8
Zygomatic width	12·1	(6) 11·9–12·1	—	—	(1) 10·5
Width of braincase	7·7	(7) 7·6–7·9	(7) 7·6–8·0	7·6	(2) 7·1, 7·1
Mastoid width	8·8	(7) 8·5–9·0	(7) 8·5–8·7	8·5	(2) 7·9, 7·9
c^1–c^1 (alveoli)	4·6	(7) 4·5–4·8	(7) 4·4–4·8	4·7	(3) 4·3–4·8
m^3–m^3	7·7	(7) 7·4–7·7	(7) 7·1–7·4	7·0	(3) 6·7–6·8
c–m^3	6·9	(7) 6·7–7·0	(7) 6·5–6·7	6·4	(3) 6·0–6·1
Length complete mandible from condyles	13·1	(7) 12·9–13·6	(4) 12·2–12·8	—	(1) 11·5
Length right ramus from condyle	13·5	(7) 13·4–14·0	(7) 12·6–13·2	12·5	(3) 11·5–11·8
c–m_3	7·3	(7) 7·1–7·4	(7) 6·9–7·2	6·9	(3) 6·3–6·5

width 6·5, 6·5, 6·5; c^1–c^1 (alveoli) 3·4, 3·3, 3·4; m^3–m^3 5·4, 5·0, 5·2; c–m^3 4·3, 4·4, 4·4; length complete mandible from condyle —, —, 8·5; length right ramus from condyle —, 8·6, 8·9; c–m_3 4·5, 4·6, 4·6.

Myotis ater (?) nugax Allen & Coolidge, 1940

Myotis abbotti nugax Allen & Coolidge. 1940 : 137. Bundutuan, Mount Kinabalu, Sabah, 3500 ft.

Specimens examined. ♂ BM(NH) 83·73 Cave near Gomantong; ♂ CMF 830414.1 Gomantong, Sabah (both in alcohol, skulls extracted).

Remarks. These specimens are referred to *nugax* Allen & Coolidge without direct comparison. They agree quite closely with the original description although in the upper jaw the second premolar (pm^3), while minute, is completely or almost completely intruded from the toothrow into a recess between pm^2 and pm^4. According to Allen & Coolidge it is absent from the holotype but otherwise slightly internal to the axis of the toothrow. In the lower jaw the second premolar (pm_3) is minute and crowded inward, as these authors remark in the initial account. A further example, BM(NH) 78.1541 from Sinoa, Sabah may also represent *nugax* but pm^3_3, although very small, are not intruded from the toothrows. Clearly more material is needed to establish variability in this feature.

In life, all specimens handled by CMF from various localities in Sabah had a distinctive coloration. The upperparts were dark brown with black bases to the fur, while the underparts were a paler grey-brown, except for a golden brown patch in the centre of the belly.

Measurements (BM(NH) 83.73, CMF 830414.1, BM(NH) 78.1541, in that order): length of forearm 40·4, 41·2, 41·4; greatest length of skull 15·6, —, —; condylobasal length 14·5, —, —; condylocanine length 13·8, —, —; basal length 13·0, —, —; palatal length 8·2, —, 7·9; least interorbital width 3·7, 3·7, 3·5; zygomatic width 9·7, 10·1, —; width of braincase 7·2, 7·4, —; mastoid width 7·7, 7·9, —; c^1–c^1 (alveoli) 3·8, 3·9, 3·8; m^3–m^3 6·3, 6·5, 6·3; i^2–m^3 6·7, 6·9, 6·8; c–m^3 5·5, 5·8, 5·7; length complete mandible from condyles ——, 11·2, ——; length right ramus from condyle 11·0, 11·3, 11·9; c–m_3 6·0, 6·3, 6·2.

Discussion. Tate (1941*a*) considered *nugax* probably to be the geographical representative in Borneo of *M. ater* (Peters, 1866) from the Molucca Islands, placing it in the subgenus *Selysius* rather than in *Leuconoe* to which its description as a subspecies of *M. abbotti* Lyon, 1916 would otherwise refer it. Subsequently, Hill (1962) provisionally associated *nugax* with *M. mystacinus* (Kuhl, 1819), being followed in this opinion by Medway (1965, 1977) who thought it to be a highland subspecies, both authors considering *ater* also to be a subspecies of *M. mystacinus*. More recently, Hill (1983) has reviewed the small-footed *Myotis* of south-eastern Asia and has concluded that *M. muricola* (Gray, 1846) is a distinct eastern species, rather than a subspecies of *M. mystacinus* as it was listed by Ellerman & Morrison-Scott (1951). This author, however, considered *ater* to be a species distinct from *muricola* and has suggested that the original opinion advanced by Tate that *nugax* should be referred to it as a subspecies may be correct. These Bornean specimens are similar to *M. ater* from the Moluccan islands of Buru and Ceram, although slightly larger in some respects than the largest of Moluccan *ater* measured by Hill (1983), and tend to confirm this view.

Pipistrellus cuprosus sp. nov.

Holotype. ♂ BM(NH) 83.351 Sepilok, Sabah, 5°52′ N, 117°56′ E. Collected 17 April 1983 by C. M. Francis. Original number CMF 830417.1. In alcohol, skull extracted.

Other material. ♂ CMF 830417.2. Other data as holotype.

Diagnosis. Similar externally and cranially to *Pipistrellus societatis* Hill, 1972 from Malaya, but differing from this species in smaller size, in more rounded, globular and less elongated braincase; in a shallower frontal depression; in wider, shallower pre-palatal emargination;

and in smaller teeth, their lingual portions in particular much reduced in comparison with the Malayan species. In some respects *P. cuprosus* resembles *P. circumdatus* (Temminck, 1840) from Java, Malaya and Burma but, apart from its considerably smaller size, like *P. societatis* it differs from this species in its more inflated frontal region, the frontal profile more nearly straight, without the distinct concavity of *P. circumdatus,* in similarly poorly defined supraorbital ridges that contrast with the more obvious ridges of that species, and in a similarly shallower, less evident frontal depression. As in *P. societatis* the narial emargination is narrower than in *P. circumdatus* and the basial pits are shallower: like *P. societatis* it differs sharply from *P. circumdatus* in its very short bony post-palate. The third upper molar (m^3) of *P. cuprosus* is a little shorter and more platelet-like than in *P. circumdatus,* as it is in *P. societatis.*

DESCRIPTION. Size small to medium (length of forearm 34·7–36·4); head short, with short, blunt, broad muzzle; ear large, its anterior margin strongly convex with well developed lobe at its base, the tip of the ear bluntly rounded; posterior margin of ear strongly convex, terminating at its insertion just behind the angle of the mouth in a prominent, wide quadrate lobe. Tragus with strongly concave anterior margin, rising to anteriorly directed point; upper margin of tragus nearly horizontal, strongly convexly curved posteriorly to posterior margin which is nearly straight, terminating basally in a large, rounded lobe. Ears quite heavily margined with dull white or yellowish white, the upper margin of the tragus similarly edged, a feature found to a greater or lesser extent in both *Pipistrellus societatis* and *P. circumdatus.* As in *P. societatis* there is a small wart bearing a few long hairs medianly situated just anterior to the throat, on a line joining the angles of the mouth. Wing inserted on the outside of the foot at the base of the fifth toe; calcar long as in *P. societatis* and *P. circumdatus,* extending along at least two thirds of the uropatagial margin; an extremely narrow post-calcarial lobe.

Pelage and pelage colour (from specimens in alcohol) similar to that of *Pipistrellus societatis* and *P. circumdatus.* Dorsal surface with pelage that is thick, dense and rather long, the hairs black or blackish brown at the base and for most of their length, liberally tipped with deep reddish orange or copper: in the two specimens examined the hairs over the entire dorsal surface are tipped with this brighter colour. Pelage over the crown of the head similarly tipped, the tipping slightly paler and more yellowish than on the back; as in *P. societatis* a small area of straw coloured or pale orange yellow hairs with dark brown tips just anterior to the junction of the medial aural margin with the head. These paler areas on each side merge into a transverse band of hairs that are narrowly dark based, then paler brown or straw coloured, with a narrow brownish sub-terminal annulation and pale yellowish orange tips, extending across the muzzle just in front of the eyes. As on the back, the fur on the crown and forehead is dense and long. Ventral pelage dark brown or brown, the hairs tipped with yellowish white on the upper part of the chest at the shoulders, otherwise with greyish white. Flight membranes black: fur extending on to the dorsal surface of the uropatagium but forearms and tibiae not haired.

In most points of coloration *Pipistrellus cuprosus* is similar to *P. societatis* or to *P. circumdatus.* All have the ear and tragus rimmed to some extent at least with dull white or yellowish white, black based or blackish brown based pelage that dorsally is tipped to a greater or lesser extent with yellowish, orange, russet or copper, and, in addition, all have dense, rather long fur. *Pipistrellus cuprosus* and *P. societatis,* however, apparently differ from *P. circumdatus* in the presence of an area of paler, straw coloured, dark tipped hairs at the anterior or medial base of the ear, and also in having a band of predominantly paler hairs extending across the muzzle just in front of the eyes. In *P. circumdatus* the black based, yellowish tipped fur extends unbrokenly between the ear bases and forward on to the muzzle. In both *P. cuprosus* and *P. societatis* the paler areas at the ear bases form the ends of the band of paler hairs that extends forward and across the muzzle. At the base of the ears in both the hairs are predominantly straw coloured, with dark tips; these blend into an anterior band of hairs that are narrowly dark based, then pale brown or straw coloured, with a sub-terminal brownish annulation, then tipped with yellowish.

Skull small, with rounded, globular and inflated braincase; postorbital region wide, curving abruptly to small supraorbital projections; supraorbital ridges weakly defined; braincase and frontal region elevated to produce a nearly straight rostral profile, with only a slight frontal concavity; rostrum broad, elevated posteriorly, with very slight median sulcus bounded laterally by low, rounded swellings; narial emargination narrow, more or less U-shaped; palate short and broad, the pre-palatal emargination wide, shallow, extending laterally just beyond the inner faces of i^{2-2} and posteriorly to a line joining the centres of the canines, in contrast to *Pipistrellus societatis* and *P. circumdatus* in which the emargination is deeper, reaching to a line joining the rear faces of these teeth; bony post-palate very short, with wide mesopterygoid fossa and blunt post-palatal spine; basial pits shallow.

Dentition much as in *Pipistrellus societatis*; inner upper incisor (i^2) slender, not massive as in that species but similarly bicuspid with small posterior cusp, lacking any small posterior cingulum cusp; outer upper incisor (i^3) very small, one quarter or less the basal area of i^2, with a central cusp flanked by small lateral cusps, its tip reaching only to the cingulum of i^2, the tooth separated from the canine by a narrow diastema and pushed forward so that the incisors lie on a straight line or nearly so, transversely to the longitudinal axis of the skull; anterior upper premolar (pm^2) minute, completely intruded into a recess between c^1 and the posterior upper premolar (pm^4), absent from CMF 830417.2, with no trace of any alveolus on either side; m^3 reduced, slightly platelet-like but third commissure and metacone present; i_1 and i_2 incipiently four-cusped as in *P. societatis*; i_3 shorter and wider than these teeth, with three cusps as in that species; anterior lower premolar (pm_2) about one quarter crown area of posterior lower premolar (pm_4) and about one half its height; in comparison with *P. circumdatus* the hypoconid and entoconid of m_3 slightly reduced.

Baculum (Fig. 1) very small, in tip of glans penis, with short, slender shaft, the tip slightly upcurved, the shaft supported by paired basal flanges separated posteriorly by a shallow, rounded emargination. The baculum is like that of *Pipistrellus societatis* but smaller: it differs from the baculum of *P. circumdatus* in its higher, more angular upper margin and more angular basal lobes.

Measurements of the holotype, followed by those of CMF 830417.2 and (in parentheses) of the holotype (BM(NH) 67.1605) and one other example (BM(NH) 81.1802) of *Pipistrellus societatis:* length of forearm 34·7, 36·4, (37·6, 39·4); greatest length of skull 13·6, 13·7, (15·3, 15·0); condylobasal length 12·9, 13·0, (14·4, 14·3); condylocanine length 12·7, 12·8, (14·1, 14·1); length orbit-gnathion 3·0, 3·1 (3·6, 3·9); palatal length, excluding post-palatal spine 6·1, 6·1, (6·6, 6·7); length post-palatal extension or bridge, excluding post-palatal spine (from a line joining rear faces of m^{3-3} to palation) 4·7, 4·8, (5·0, 5·1); width across anteorbital foramina 4·7, 4·7, (5·1, 5·2); lachrymal width 6·1, 6·2 (6·7, 6·8); width across supraorbital tubercles 5·5, 5·8, (6·0, 6·0); least interorbital width 4·1, 4·1, (4·3, 4·3); zygomatic width 9·6, 10·1, (10·4, 10·5): width of braincase 7·4, 7·7, (7·9, 7·5); mastoid width 7·6, 8·0, (8·5, 8·4); c^1–c^1 (alveoli) 4·3, 4·4, (4·6, 4·8); m^3–m^3 6·5, 6·4, (6·7, 7·0); c–m^3 4·9, 4·8, (5·2, 5·5); length complete mandible from condyles 9·4, 9·5, (10·4, 10·6); length right ramus from condyle 9·9, 10·0, (10·8, 11·0); c–m_3 5·2, 5·3, (5·6, 5·9)

ETYMOLOGY. The specific name alludes to the coppery bronze tipping of the dorsal pelage of this attractive new species.

DISCUSSION. Heller & Volleth (1984) have examined five examples of *Pipistrellus societatis* from the Ulu Gombok Field Studies Centre, near Kuala Lumpur, Selangor, Malaya. Without direct comparison they consider *societatis* to be a lowland subspecies of *P. circumdatus.* Their measurements, however, demonstrate quite clearly the short palate (palatal length 6·7–6·9 in *societatis,* 7·6–8·6 in *circumdatus*) and the short bony post-palate (length palatal extension or bridge 5·1–5·4 in *societatis,* 6·1–6·8 in *circumdatus*) that are among the most obvious distinguishing features of *societatis,* and also its considerably shorter toothrows (c–m^3 5·3–5·6 in *societatis*, 5·9–6·4 in *circumdatus*; c–m_3 5·5–5·9 in *societatis*, 6·3–6·7 in *circumdatus*). Moreover, other distinguishing features have been indicated in this account and these, together with the discovery of a smaller species clearly more closely allied to *societatis* than to *circumdatus* suggest that *societatis* should be retained as a distinct species.

In the same study Heller & Volleth have examined the karyological features and baculum of *Pipistrellus societatis*, transferring these to *P. circumdatus* (which they have not seen) as a consequence of their inclusion of this taxon in that species. According to these authors these features indicate that *P. circumdatus* (sic) should be transferred to *Eptesicus*, the presence or absence of the anterior upper premolar (pm^2) having proved unreliable as a diagnostic character separating *Pipistrellus* and *Eptesicus*. Indeed, this tooth is absent from one of the specimens of *P. societatis* that they examined, as it is from one of those of *P. cuprosus* here described. Instability of this character is of course well known in certain species of *Pipistrellus*.

The karyological evidence advanced by Heller & Volleth cannot be readily evaluated since many of the species of these nominal genera remain to be studied. The baculum (Fig. 1) of *P. societatis*, however, differs in some respects from that of *P. circumdatus*, but both are similar to that of *P. subflavus* from North America. Both differ from the more triangular baculum often associated with *Eptesicus* in the presence of a short shaft. On a wider front Heller & Volleth also transfer the Australian *Eptesicus douglasi, E. pumilus, E. vulturnus, E. regulus* and *E. sagittula* to *Pipistrellus*, together with the African *E. capensis*, the first four of these at least having bacula of the long shafted type that characterizes many species of that genus. Current studies of the bacula of the nominal genera *Pipistrellus* and *Eptesicus* in London and Sevenoaks (the Harrison Zoological Museum) indicate a wide variety of bacular structure and in these circumstances we prefer to retain the *circumdatus* group (and thus *circumdatus, societatis* and *cuprosus*) in *Pipistrellus*, at least until this matter is more fully resolved.

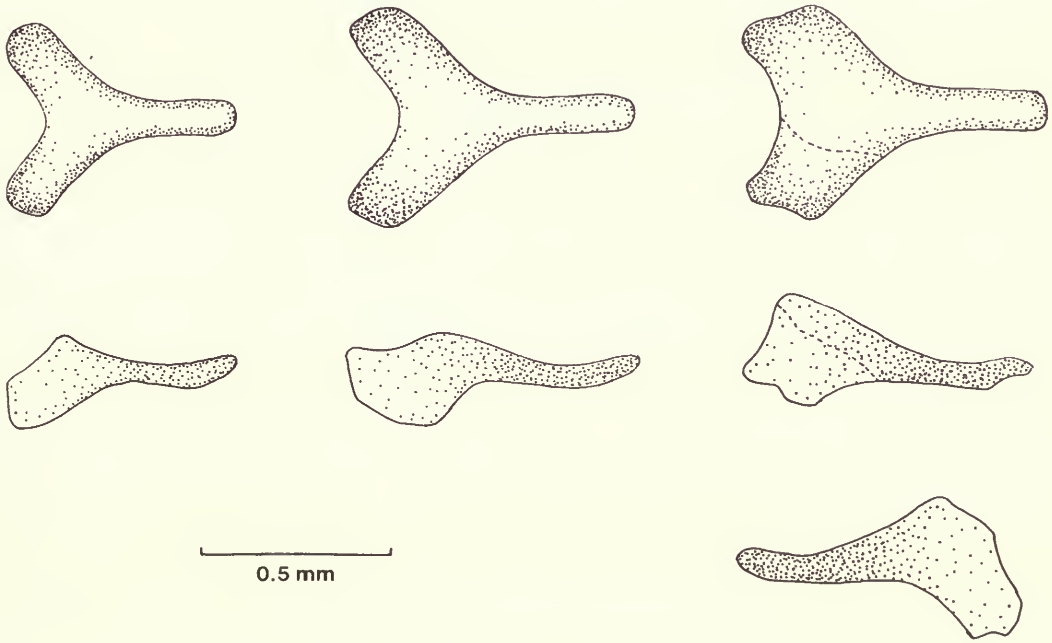

Fig. 1 Dorsal (above) and lateral (below) aspect of the baculum of: left, *Pipistrellus cuprosus*, BM(NH) 83.351, holotype, Sabah; right, *P. societatis*, BM(NH) 67.1605, holotype, Malaya; and centre, *P. circumdatus*, BM(NH) 73.618, Malaya. Lateral aspect is of right face of baculum except for *P. societatis*, both lateral faces of the damaged baculum being illustrated. (*Pipistrellus societatis, P. circumdatus* from drawings prepared by D. L. Harrison, Harrison Zoological Museum, Sevenoaks, England.)

Pipistrellus macrotis (Temminck, 1840)

Vespertilio macrotis Temminck, 1840 : 218. Padang, Sumatra.

Specimen examined. ♂ CMF 830901.1 Kuala Selangor, Malaya (in alcohol, skull extracted).

Remarks. This specimen is the first of *Pipistrellus macrotis* to be recorded from Malaya. It corresponds closely with the original description by Temminck: like the closely related *P. vordermanni* (Jentink, 1890) from Billiton Island and Borneo it may be recognized readily by its large ears, slightly hatchet-shaped tragus with anteriorly directed point, and by its white or whitish wings. As in *P. vordermanni* the skull is short with a rather globose braincase and a short, broad rostrum with small supraorbital tubercles, strong zygomata that are well developed jugally, and deep basioccipital pits. The anterior upper premolar (pm^2) is very small, completely intruded into a recess between the canine and the posterior upper premolar (pm^4), as in *P. vordermanni,* while the anterior lower premolar (pm_2) is similarly much reduced.

Measurements: length of forearm 33·5; length of ear 14·1; greatest length of skull 12·4; condylobasal length 11·7, condylocanine length 11·5; width across supraorbital tubercles 4·6; zygomatic width 8·5; least interorbital width 3.7; width of braincase 6·6; mastoid width 7·4; c^1–c^1 (alveoli) 4·3; m^3–m^3 5·4; c–m^3 4·1; length complete mandible from condyles 8·0; length right ramus from condyle 8·4; c–m_3 4·3.

Discussion. This Malayan example of *P. macrotis* is in good agreement with a single specimen (BM(NH) 23.1.2.12) from Sebang, Sumatra, measured by Hill (1983). Like this Sumatran example, it differs from *P. vordermanni* from Borneo only in slightly larger size and in rather whiter wings. As in Bornean *P. vordermanni* the translucent uropatagium is tinged with brown. *Pipistrellus curtatus* Miller, 1911 from Engano Island also seems very close to *P. macrotis* and it seems evident that an adequate representation of the three taxa might show them to be conspecific.

Philetor brachypterus verecundus (Chasen, 1940)

Eptesicus verecundus Chasen, 1940 : 53. Mount Kledang, Perak, Malaya, 2646 ft.

Specimen examined. ♀ BM(NH) 83.352 Sepilok, Sabah (in alcohol, skull extracted).

Remarks. Bornean records of *Philetor brachypterus* were reviewed by Hill (1983): this specimen represents the fourth reported occurrence of the species in Borneo and the second report from Sabah, there being a previous record from Poring, Kinabalu National Park at Ranau. This female from Sabah agrees favourably in cranial size with the female holotype (BM(NH) 47.1437) of *P. b. verecundus* and with female examples from Nepal and Malaya measured by Koopman (1983).

Measurements: length of forearm 32·1; greatest length of skull 14·1; condylobasal length 13·8; condylocanine length 13·3; width across anteorbital foramina 4·7; width across supraorbital tubercules 7·1; least interorbital width 4·5; zygomatic width 10·0; width of braincase 7·8; mastoid width 8·8; c^1–c^1 (alveoli) 5·0; m^3–m^3 7·1; c–m^3 4·5; length complete mandible from condyles 9·6; length right ramus from condyle 10·1; c–m_3 4·7.

Hesperoptenus blanfordi (Dobson, 1877)

Vesperugo (Hesperoptenus) blanfordi Dobson, 1877 : 312. Tenasserim, Burma.

Specimens examined. ♂♂ BM(NH) 83.353, CMF 830410.4 Sepilok, Sabah (in alcohol, skulls extracted); ♀ CMF 821229.2 Sepilok Laut, Sabah (in alcohol, skull not available); ♀♀ CMF 0029–0031 Witti Range (in alcohol, skulls extracted).

Remarks. There is no previous record of *Hesperoptenus blanfordi* from Borneo, the species being known hitherto from Burma, Thailand and Malaya. Hill (1976) examined the species in some detail. It may be readily recognized by its small size, densely haired internarial region and anteriorly directed, pointed tragus; the upper surface of the forearm is densely haired and there is a broad, cushion-like pad at the base of the thumb; the braincase is flattened and the small outer upper incisor (i^3) is inwardly displaced to lie behind the inner tooth (i^2), alongside the antero-internal face of the canine. These Bornean examples are smaller in some respects than Thai and Malayan specimens measured by Hill (1976) and sometimes have slightly smaller teeth, especially the inner upper incisors (i^{2-2}) and canines, although closely approached in this by some continental examples.

External measurements of six specimens: length of forearm 24·2–26·4; thumb (c.u.) 3·8–4·0; II^m 23·0–24·4; III^m 23·4–25·6; III^1 12·6–14·3; III^2 7·6–8·5; IV^m 23·4–24·9; V^m 22·8–24·1.

Cranial measurements of five specimens (except where indicated in parentheses): greatest length of skull 12·1–12·6; condylocanine length 11·4–11·8; condylobasal length 11·2–11·6; length orbit-gnathion 2·9–3·1; width across anteorbital foramina 4·6–4·9; width across front of orbits 5·7–6·1; width across supraorbital swellings 5·8–6·0; zygomatic width —; least interorbital width 4·4–4·6; width of braincase 7·2–7·5; height of braincase 4·4–4·9; mastoid width 7·3–7·7; c^1–c^1 (alveoli) 3·9–4·1; m^3–m^3 5·5–6·1; c–m^3 4·0–4·2; length complete mandible from condyles 8·1–8·3 (3); length right ramus from condyle 8·7–8·9 (4); c–m_3 4·4–4·5.

The baculum (Fig. 2) of *Hesperoptenus blanfordi* has not hitherto been examined: those of the remaining species excepting *H. gaskelli* Hill, 1983 were described and illustrated by Hill (1976). Baculum with long, slender, ventrally fluted shaft, the tip expanded both vertically and horizontally, its base expanded into broad, paired flanges separated by a shallow V-shaped aperture. The baculum of *H. blanfordi* combines some features of that of *H. doriae* which has a similar slender shaft with a transversely convex upper surface and a slightly transversely concave lower surface with those of *H. tomesi* in which the baculum has similarly well developed paired basal flanges.

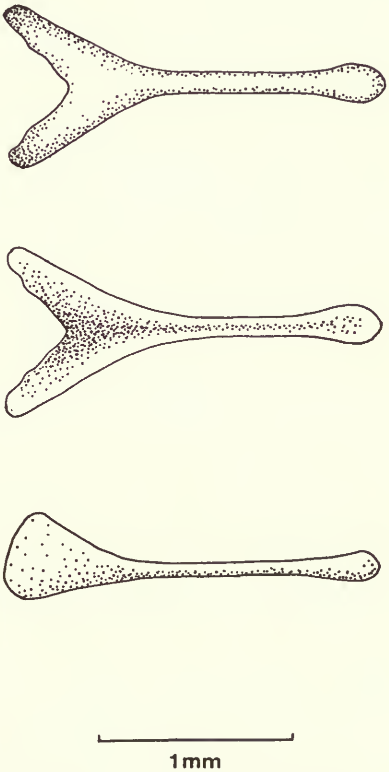

Fig. 2 Dorsal (above), ventral (centre) and right lateral (below) aspect of the baculum of *Hesperoptenus blanfordi,* CMF 830410.4, Sabah.

Hesperoptenus tomesi Thomas, 1905

Hesperoptenus tomesi Thomas, 1905 : 575. Malacca. Malaya.

SPECIMENS EXAMINED. ♀, ♂ CMF 821021.1–2 Lumerau, Sabah (in alcohol, skull of CMF 821021.1 extracted).

REMARKS. There is but one previous record of *Hesperoptenus tomesi* from Borneo, based on a juvenile male example from the Sapagaya Forest Reserve, Sabah, at 5°37′ N, 118°04′ E. Initially reported as *H. doriae* by Davis (1962), this specimen proved on further examination to represent *H. tomesi* (Hill, 1972, 1976). These specimens from Lumerau confirm the occurrence of the species in Sabah: in size they agree closely with Malayan examples measured by Hill (1976).

Measurements (CMF 821021.1–2, skull of 821021.1): length of forearm 53·2; 52·8; greatest length of skull 21·5; condylocanine length 20·5; condylobasal length 20·4; length orbit-gnathion 5·3; width across anteorbital foramina 7·5; width across front of orbits 10·7; width across supraorbital swellings 9·4; zygomatic width 15·5; least interorbital width 5·8; width of braincase 10·5; height of braincase 7·8; mastoid width 12·2; c^1–c^1 (alveoli) 8·0; m^3–m^3 10·6; c–m^3 8·5; length complete mandible from condyles 16·0; length right ramus from condyle 16·8; c–m_3 9·5.

Murina suilla (Temminck, 1840)

Vespertilio suillus Temminck, 1840 : 224, pl. 56, figs 4–6. Tapos, Java.

SPECIMENS EXAMINED. 2♂♂, 2♀♀ CMF 830325.2, 830413.1, 0043, 830804.8 Gomantong; ♂ CMF 0127 Sepilok; ♀ CMF 830114.6 Segarong; ♂ CMF 821222.3 Silau Silau Trail, Mount Kinabalu, 5000 ft, all Sabah (all in alcohol, skulls of CMF 830325.2, 830413.1, 830114.6, 821222.3 extracted); ♂ Rijksmuseum van Natuurlijke Historie (RMNH) 32236 Near Poring hot springs, Kinabalu National Park, Sabah, c. 600 m (in alcohol, coll. F. Rozendaal).

REMARKS. Medway (1977) quotes records of *Murina suilla* from Peleben, Sungei Kayan and from the lower Sungei Mahakam, both localities in East Kalimantan.

Measurements of eight specimens and four skulls (except where indicated): length of forearm 28·8–30·2; greatest length of skull 14·1–14·6; condylobasal length 12·6–13·3 (3); condylocanine length 12·1–12·8 (3); length orbit-gnathion 3·8–4·0; palatal length 6·7–7·3; width across anteorbital foramina 3·7–3·9; rostral width at lachrymals 4·7–5·0; least interorbital width 3·9–4·1; zygomatic width 8·0–8·5; width of braincase 7·0–7·1; height of braincase 6·0–6·2 (3); mastoid width 7·3–7·4 (3); c^1–c^1 (cingula) 3·6–3·7, (alveoli) 3·5–3·6; m^3–m^3 5·0–5·1; c–m^3 4·7–4·9; length complete mandible from condyles 9·1–9·6; length right ramus from condyle 9·6–10·0; c–m_3 5·2–5·5.

Murina cyclotis peninsularis Hill, 1964

Murina cyclotis peninsularis Hill, 1964 : 55. Ulu Chemperoh, near Janda Baik, Bentong District, Pahang, Malaya, c. 3°18′ N, 101°50′ E, 2000 ft.

SPECIMENS EXAMINED. ♀ CMF 8307 Sepilok, Sabah (in alcohol, skull extracted); ♂ CMF 830131.2 Lumerau, Sabah (in alcohol).

REMARKS. *Murina cyclotis peninsularis* was first recorded from Borneo by Hill (1983) who reported two specimens, one from the Gunung Mulu National Park in Sarawak and the other from Sepilok in Sabah.

Measurements (CMF 8307, 830131.2, skull of 8307): length of forearm 36·0, 37·8; greatest length of skull 18·2; condylobasal length 16·9; condylocanine length 16·2; length orbit-gnathion 4·5; palatal length 9·3; width across anteorbital foramina 4·8; rostral width at lachrymals 6·0; least interorbital width 4·5; zygomatic width 10·8; width of braincase 8·0; height of braincase 7·4; mastoid width 9·0; c^1–c^1 (cingula) 5·0, (alveoli) 4·7; m^3–m^3 5·8; c–m^3 5·9; length complete mandible from condyles 12·5; length right ramus from condyle 12·8; c–m_3 6·5.

Murina aenea Hill, 1964

Murina aenea Hill, 1964 : 57. Ulu Chemperoh, near Janda Baik, Bentong District, Pahang, Malaya, c. 3°18′ N, 101°50′ E, 2000 ft.

Specimens examined. ♂♂ BM(NH) 83.359, CMF 830105.2 Sepilok; ♀ CMF 830117.1 Segarong; ♂♂ CMF 830628.3–4 Rinangisan, all Sabah (all in alcohol, skulls of BM(NH) 83.359, CMF 830105.2, 830117.1, 830628.3 extracted).

Remarks. This species has not before been reported from Borneo, being known hitherto only from the holotype and from a second specimen (now BM(NH) 75.2148) from Ulu Gombok, 16 m NE of Kuala Lumpur, Selangor, Malaya, reported by Sly (1975), but who gave few details of the specimen. This second Malayan example is very similar to the male holotype but the bronze tipping of the pelage on the lower back is slightly eroded: the specimen has, however, a prominent 'fringe' of longer, bronze-ochraceous hairs along the base of the tail membrane, a feature that is lacking from the holotype, and in some respects its skull is slightly larger than that of the holotype. These Bornean examples, although preserved in alcohol, display nevertheless the dark based, bronze tipped dorsal pelage of *Murina aenea,* sometimes with a 'fringe' of longer hairs that are more heavily tipped with bright bronze ochraceous along the base of the tail membrane. Ventrally the pelage is basally dark brown, tipped anteriorly with buffy or pale buff brown and posteriorly usually with a more ochraceous tinge.

Measurements of five specimens and four skulls (except where indicated), followed by those of the second Malayan example (BM(NH) 75.2148): length of forearm 35·4–37·9, 35·0: greatest length of skull 16·7–17·6; 17·5; condylobasal length 15·3–16·1, 15·9; condylocanine length 14·7–15·7, 15·4; palatal length 8·3–8·6 (3), 8·6; length orbit-gnathion 4·2–4·3, 4·4; width across anteorbital foramina 4·5–4·8, 4·6; rostral width at lachrymals 5·6–6·0, 5·8; least interorbital width 4·2–4·6, 4·7; zygomatic width 10·3–10·5, 10·7; width of braincase 7·6–8·2, 7·7; height of braincase 6·8–6·9, 6·6; mastoid width 8·3–8·9, 8·6; c^1–c^1 (cingula) 5·1, 5·0, (alveoli) 4·7–4·8, 4·8; m^3–m^3 6·2–6·3, 6·2; c–m^3 5·7–6·0; 6·0; length complete mandible from condyles 11·5–11·7, 12·0; length right ramus from condyle 12·0–12·1, 12·4; c–m_3 6·3–6·5, 6·7.

Murina rozendaali sp. nov.

Holotype. ♂ BM(NH) 83.360 Gomantong, Sabah, 5°31′ N, 118°04′ E. Collected 25 April 1983 by C. M. Francis. Original number CMF 830325.1. In alcohol, skull extracted.

Other material. ♀ CMF 830403.1 From the type locality (in alcohol, skull extracted); ♀ Rijksmuseum van Naturlijke Historie (RMNH) 32235 Near Poring hot springs, Kinabalu National Park, Sabah, *c.* 600 m (in alcohol, skull extracted; coll. F. Rozendaal).

Diagnosis. Externally very similar to *Murina aenea* Hill, 1964 from Malaya but slightly smaller, the pelage longer, more lank and less close and dense; skull like that of *M. aenea* but considerably smaller and narrower, the braincase smaller and less inflated, the rostrum lower and less massive; anterior narial and pre-palatal emarginations shallower and relatively wider; anteorbital foramen separated from orbit by a narrow, not broad bar of bone as it is in *M. aenea*; zygomata much less sharply expanded; post-palatal extension narrower; mandible much less massive than in *M. aenea,* with slender, linear angular process rather than the massive, quadrangular structure of that species; and coronoid process low and broad, not high as in *M. aenea*. Externally *M. rozendaali* is similar to *M. aurata* from the continental mainland but differs from this species in its white, not dark ventral surface; in greater cranial size; in a broader rostrum with the upper toothrows not strongly convergent anteriorly but instead more nearly parallel; in the position of the outer upper incisors (i^{3-3}) which lie more nearly alongside the inner teeth (i^{2-2}) rather than behind them, the front faces of the four teeth lying almost on a transverse line across the longitudinal axis of the skull; and in having the anterior premolars ($pm\frac{2}{2}$) very much less reduced.

DESCRIPTION. Size small (length of forearm 32·1–33·1); nostrils strongly tubular; muzzle slightly swollen laterally, the swellings bearing a number of long vibrissae; ear long and broad, the anterior margin strongly convex, with a small quadrangular lobe at its base, the tip rounded; posterior margin distally convex above an angular notch, curving convexly below this notch to an angular insertion on the head above and some distance behind the angle of the mouth. Tragus long, its length about one half of the length of the ear, acutely pointed, its anterior margin straight for most of its length but slightly convex just below tip; posterior margin slightly concave just below tip but otherwise straight to widest part of tragus, distally faintly serrated; below widest point tragus narrowing abruptly to a small projection on its posterior margin, just above the base.

Pelage both dorsally and ventrally long and woolly; on face, crown, nape and back (from specimens in alcohol) hairs dark brown based, heavily tipped anteriorly with shining golden brown, bronze or ochraceous bronze, the tipping on the lower back slightly less extensive and of a slightly darker bronze hue; hairs on flanks beneath wing insertion similarly dark based but with buffy white tips, on remainder of ventral surface from chin, throat and chest to inguinal region hairs white to the base, sometimes tinged with buffy. Dorsal surface of forearm with a sprinkling of bright golden brown hairs, dorsal surface of tail, tibiae and feet quite densely clothed with longer hairs of a similar colour; dorsal surface of uropatagium with a moderate covering of long, bright brown or golden brown hairs. The overall coloration is very similar to that of *Murina aenea* but the ventral pelage is more extensively white based, and the fur on the tail, tibiae and feet is rather longer.

Skull with narrow braincase, wide interorbital region and short, narrow rostrum; a shallow frontal depression; narial emargination short and wide, shallowly U-shaped; zygomata narrow, not flaring sharply from the sides of the skull; anteorbital foramen only narrowly separated; palate narrow, with wide, shallow U-shaped anterior emargination extending posteriorly to a line joining the centres of the canines; upper toothrows only slightly convergent anteriorly; post-palatal extension narrow, with V-shaped palation, its apex broad with a small median post-palatal spicule; shallow basioccipital pits. Mandible with narrow, rather slender horizontal ramus, the angular process narrow and linear, the coronoid process rather low, broad, with a wide, rounded tip.

Inner upper incisor (i^2) small, with large main cusp and a trace of a posterior cusp; outer upper incisor (i^3) much larger, about twice or a little more as massive as the inner tooth, with small postero-internal cusp, situated almost alongside i^2 so that the anterior faces of the incisors lie almost on a straight line across the longitudinal axis of the skull; posteriorly i^3 is pressed tightly against the canine, which is not especially large and lacks any well developed cingulum on its anterior, internal or posterior faces. Anterior upper premolar (pm^2) equal in crown area to a little more than one half of the crown area of the second upper premolar (pm^4) and about equal to this tooth in height; pm^4 equal in crown area to a little less than two thirds the crown area of the first upper molar (m^1), unlike *Murina aenea* in which the crown area of pm^4 almost equals that of m^1; upper molars (m^{1-3}) with no especial peculiarities. Lower incisors small, imbricated, i_1 and i_2 clearly tricuspid, i_3 with three irregular, poorly developed surface cusps, i_{1-2} about half as wide as long, i_3 almost as wide as long; lower canine with narrow internal cingulum; crown area of anterior lower premolar (pm_2) about half that of the second lower premolar (pm_4), of pm_4 a little more than one half of the crown area of the first lower molar (m_1); hypoconids and entoconids of m_{1-2} clearly apparent and distinct, separated from the protoconids and metaconids by a wide and moderately excavated trough.

Measurements of the holotype, followed by those of CMF 830403.1 and RMNH 32235, in that order: length of forearm 32·1, 32·3, 33·1; length of ear 12·6, 13·2, 12·8; length of tibia 17·8, 18·0, 17·9; length of foot (c.u.) 8·5, 8·5, 8·8; greatest length of skull 15·7, 15·6, 16·0; condylobasal length 14·4, 14·4, 14·6; condylocanine length 14·1, 14·0, 14·0; palatal length 7·8, 7·7, 8·0; length orbit-gnathion 3·9, 4·0, 4·1; width across anteorbital foramina 4·4, 4·3, 4·4; rostral width at lachrymals 4·9, 4·8, 5·0; least interorbital width 4·1, 4·2, 4·1; zygomatic width 9·1, 9·4, 9·3; width of braincase 7·3, 7·5, 7·5; height of braincase 6·2, 6·1, 6·1; mastoid width 7·5, 7·8, 7·8; c^1–c^1 (cingula) 4·1, 4·0, 4·4, (alveoli) 3·8, 3·7, 4·1; m^3–m^3 5·4, 5·4, 5·5; c–m^3 5·2, 5·3, 5·6; length complete mandible from condyles 10·5, 10·5, 10·4; length right ramus from condyle 10·9, 10·9, 10·9; c–m_3 6·0, 5·9, 6·1.

ETYMOLOGY. This species is named after Mr Frank Rozendaal of the Rijksmuseum van Natuurlijke Historie, Leiden, who while visiting the Kinabalu National Park in Sabah collected the first specimen to be obtained.

DISCUSSION. The genus *Murina* was briefly reviewed by Tate (1941*b*), who provided a key with notes on selected species. Since then Hill (1964) has examined its members in south-eastern Asia, with the description of a further subspecies of *M. cyclotis* (*M. c. peninsularis*) and of a further species (*M. aenea*) from Malaya, while Van Deusen (1961) and Hill (1983) have reviewed the forms occurring east of Wallace's Line. Yoshiyuki (1970) has described *M. tenebrosa* from the Tsushima Islands and more recently (1983) has proposed *M. silvatica* for members of the *aurata* group from Japan, and Maeda (1980) has reviewed *M. aurata* and its associated forms. Currently as few as eleven (Corbet & Hill, 1980) or as many as fifteen (Honacki *et al.*, 1982) species of *Murina* are recognized, excluding the more recently described *M. silvatica* Yoshiyuki, 1983.

Specimens in the British Museum (Natural History) indicate that the members of the genus so far examined fall cranially and more especially dentally into two groups. One is of generally small species in which the rostrum is rather narrow and the upper toothrows markedly convergent anteriorly. The inner upper incisor (i^2) lies distinctly anterior to the outer upper incisor (i^3), with its postero-external face abutting the antero-internal face of i^3, and the anterior premolars (pm^2_2) are much reduced. The group includes *leucogaster, aurata, florium, suilla* (including *canescens* and *balstoni*), and probably also *ussuriensis, tenebrosa* and *silvatica*, but these latter three have not been examined. Although in most respects in good agreement with this group, *tubinaris* has upper incisors that begin to approach those of the second group. In this group the rostrum is broad anteriorly, the toothrows more nearly parallel, and i^3 is situated more laterally to i^2 so that at the extreme its inner face lies more or less alongside the outer face of that tooth, with pm^2_2 less reduced. This group includes *huttonii, cyclotis, aenea* and *rozendaali*: the incisors of *huttonii* and *cyclotis* are similar in relative position to those of *tubinaris* but in *aenea* and *rozendaali* i^3 lies almost totally alongside the outer face of i^2. There is thus a gradual change in the position of i^3 in relation to i^2, perhaps related to shortening and broadening of the rostrum: in *M. cyclotis cyclotis* i^3 is situated partly alongside and partly behind i^2 but in the larger *M. c. peninsularis* which has a rather broader rostrum i^3 tends in position towards the more extreme condition of *aenea* or *rozendaali*. The new species belongs quite clearly to the latter group: like *M. aenea*, to which it appears closely related, in its external appearance it resembles *M. aurata*, but, like *M. aenea*, it differs sharply from that species in the details of its cranial and dental architecture.

Harpiocephalus (?) mordax Thomas, 1923

Harpiocephalus mordax Thomas, 1923 : 88. Mogok, Upper Burma.

SPECIMEN EXAMINED. ♀ CMF 0099 Sepilok, Sabah (in alcohol, skull extracted).

REMARKS. The genus *Harpiocephalus* has been recorded once before from Borneo, by Medway (1977) who referred a specimen from Quoin Hill Cocoa Research Station, near Tawau, Sabah to *H. harpia* (Temminck, 1840). Medway remarked that the specimen was assigned to the nominate subspecies *H. h. harpia* on the basis of Tate's (1941*b*) description of a near topotype from Java, which it closely resembled in all salient characters. The specimen was first reported without taxonomic comment by Tan (1966) who examined its stomach contents.

This old adult specimen from Sepilok, however, agrees much more readily with *Harpiocephalus mordax* Thomas, 1923, described from Burma and represented in London only by the holotype (BM(NH) 4.4.27.1) and by one other specimen (BM(NH) 4.4.27.2), also from the type locality. This species was characterized by Thomas as having the skull markedly larger than in *H. harpia*, with bigger crests and more widely expanded zygomata, the muzzle much developed, and broad and heavy. According to Thomas, the anterior teeth, the incisors and canines are much enlarged, very stout and heavy, and even the premolars are slightly broader than the first molar, being narrower in *H. harpia*. The posterior molar was said to be not quite so minute as in the latter.

The specimen from Sepilok complies in most respects with this definition: in particular the muzzle is much broadened and more massive in comparison with the limited series of *Harpiocephalus harpia* in London, and the zygomata are much more widely expanded. The anterior teeth, especially the canines, are heavier and altogether more massive than in *H. harpia*. Re-examination of the two original specimens studied by Thomas suggests, however, that the cranial crests are little more developed in *mordax* than in the oldest of *H. harpia* and that although cranially *H. mordax* is larger in most respects than *H. harpia*, its greatest size differences are clearly chiefly those that relate to the width of the muzzle and zygomata. The Bornean example differs from Burmese *H. mordax* in the smaller size of m^3, which in this specimen is reduced to little more than a mere flake. In life, this specimen was conspicuous for its bright orange coloration.

Measurements of CMF 0099, with those of the holotype of *Harpiocephalus mordax* and of the second Burmese example, in that order, followed (in parentheses) by the measurements of five examples of *H. harpia* from Java and of the lectotype and topotypes of *harpia* (five specimens except where indicated) as measured by Husson (1955): length of forearm 48·2, 54·1, 50·7, (43·4–49·7; (4) 45·0–49·5); greatest length of skull 22·3, 23·2, 22·4, (20·6–22·3; (4) 20·4–21·6); condylobasal length 20·6, 21·1, 20·3, (18·4–20·3; (4) 18·8–19·8); condylocanine length 19·8, 20·3, 19·7, (18·0–19·5; (4) 18·3–19·1); basal length 18·1, 18·9, 18·4, (16·4–18·4; (3) 17·3–17·5); palatal length 11·4, 12·3, 11·3, (10·4–11·6; (4) 11·0–11·7); length palatal bridge (from rear of incisive foramen to palation) 9·3, 10·4, 9·2, (8·7–9·6; —); width across anteorbital foramina (? lachrymal width of Husson) 7·3, 6·8, 6·8, (5·9–6·5; 5·8–6·2); width across supraorbital tubercles 8·3, 8·1, 7·9, (7·0–7·7; —); least interorbital width 5·3, 5·5, 5·6, (5·3–5·7; 5·3–5·7); zygomatic width 14·6, 14·3, 14·9, (12·5–13·7; 13·1–13·6); width of braincase 10·2, 9·6, 9·9, (9·2–9·8; (4) 9·2–10·1); height of braincase 8·8, 8·9, 9·2, (8·4–8·9; (4) 8·6–8·8); mastoid width 12·0, 11·5, 11·8, (10·3–11·6; (3) 10·5–11·2) c^1–c^1 (alveoli) 7·8, 7·1, 7·2, (6·1–6·6; —); (cingula) 7·5, 7·2, 7·3, (6·1–6·6; 6·2–6·7); m^2–m^2 8·0, 7·7, 7·7, (6·9–7·4; 7·2–7·3); c–m^3 6·9, 7·4, 7·2, (6·3–6·5; 6·7–6·9); length complete mandible from condyles 15·4, 16·1, 15·6, (13·9–15·0; —); length right ramus from condyle 16·1, 16·5, 16·2, (14·3–15·6; 14·5–15·6); coronoid height 9·5, 9·2, 9·3, (7·8–8·5; 7·6–8·6); c–m_3 ·8·0, 8·3, 8·2, (7·4–7·9; 7·7–7·8).

The specimen from Quoin Hill Cocoa Research Station reported by Medway (1977) as *Harpiocephalus harpia* is in the collections of the University of Malaya. It is a mature if not somewhat aged individual, its teeth quite worn. In size and especially in the width of the skull it agrees closely with specimens of *H. harpia* from Java: length of forearm 47·7; greatest length of skull 22·1; c^1–c^1 (alveoli) 6·0; m^2–m^2 7·1; c–m^3 6·6.

DISCUSSION. The systematics of *Harpiocephalus* remain unclear. The genus is generally poorly represented in collections and appears to be rarely collected. It was last examined in any detail by Tate (1941*b*) who described specimens from Java and northeastern India and who gave notes on the supposed type material of *H. harpia* in the Rijksmuseum van Natuurlijke Historie, Leiden: this was later examined by Husson (1955) who designated a lectotype.

Ellerman & Morrison-Scott (1951) considered the genus to be monospecific, with four definite subspecies, namely *Harpiocephalus harpia harpia* (Temminck, 1840) in the eastern part of the range from Sumatra and Formosa east to the Molucca Islands, *H. h. rufulus* Allen, 1913 from Indochina, *H. h. lasyurus* (Hodgson, 1847) from northeastern India, and *H. h. madrassius* Thomas, 1923 from southern India. These authors thought *mordax* to be a possible subspecies of *H. harpia*. More recent compilers (Corbet & Hill, 1980, Honacki *et al.*, 1982) have followed this lead and have listed *Harpiocephalus* with but a single species. The material available is quite inadequate to establish the extent of individual variation. However, neither the holotype nor the paratype of *H. mordax* is an especially old individual, and an example (BM(NH) 9.1.5.359) of *H. harpia harpia* in the collections in London, of similar age, shows no evidence of rostral widening to resemble *H. mordax*. The Burmese, Bornean and most of the Javan and other specimens examined are female but there is no suggestion of rostral broadening in one male (BM(NH) 9.1.5.356) of *H. h. harpia* from Java or in another (BM(NH) 16.7.29.42) of *H. h. lasyurus* from northeastern India. The principal distinguishing characteristic of *H. mordax* does not therefore appear to be an age or sex related feature.

Kerivoula minuta Miller, 1898

Kerivoula minuta Miller, 1898 : 321. Trong (=Trang), Peninsular Thailand.

Specimens examined. ♂ BM(NH) 82.558, ♀ CMF 0051 Gomantong (in alcohol, skulls extracted); ♂♂ CMF 830221.1, 830223.1–3 Baturong (in alcohol, skulls extracted); ♂♂ CMF 821106.01, 821107.06 in alcohol, skulls extracted but not available in London), 821127.5–6 (in alcohol, skull of 821127.5 extracted) Madai; ♂ CMF 0028 Witti Range (in alcohol), ♀ CMF 830113.1 (in alcohol, skull extracted but not available in London), ♂♂ 830114.8 (in alcohol, skull extracted), 830114.9 (in alcohol, skull extracted but not available in London) Segarong; ♂♂ BM(NH) 83.354–355 (in alcohol, skulls extracted), CMF 821017.1 (alcohol, skull extracted but not available in London) Lumerau; ♂♂ CMF 821022.2–3 Silabukan (in alcohol, skulls extracted but not available in London); all in Sabah.

Remarks. Medway (1977) first recorded *Kerivoula minuta* from Borneo on the basis of a single specimen (now BM(NH) 76.307) obtained 12 miles N of Kalabakan, Tawau, Sabah. These further specimens confirm this initial report and agree closely with those from Malaya reported by Hill (1965). The smallest examples of this species are little larger than *Craseonycteris thonglongyai* Hill, 1974*b*, generally accepted as among the smallest if not the smallest of bats.

Measurements appear in Table 4.

Kerivoula intermedia sp. nov.

Holotype. ♂ BM(NH) 83.356 Lumerau, Sabah, 5°12′ N, 118°52′ E. Collected 6 February 1983 by C. M. Francis. Original number CMF 830206.4. In alcohol, skull extracted.

Other material. Sabah: ♀, ♂ CMF 821016.3–4, ♀♀ 821021.4–5 (in alcohol, skulls extracted but not available in London), ♀ BM(NH) 83.357 (in alcohol, skull extracted). From the type locality. ♂, ♀ CMF 0013, BM(NH) 82.559 (in alcohol, skulls extracted), ♂♂, ♀ CMF 830103.1–3, ♂ 830108.1 (in alcohol skulls extracted but not available in London) Sepilok; ♂♂ BM(NH) 82.560 (in alcohol, skull extracted, ♂♂ CMF 0026–0027 (in alcohol) Witti Range; ♀ CMF 821022.1 Silabukan (in alcohol, skull extracted but not available in London).

Malaya: ♂ BM(NH) 71.1134 Tekam Forest Reserve, Jerantut, Pahang; ♀ BM(NH) 75.1295 Sungei Kelembang Camp, Ulu Setiu, Besut, Trengganu, c. 5°25′ N, 116°30′ E (both in alcohol, skulls extracted).

Diagnosis. Externally, cranially and dentally similar to *Kerivoula minuta* Miller, 1898 from Malaya and Borneo, but skull larger, intermediate in size between *K. minuta* and *K. pellucida* (Waterhouse, 1845); differs from *K. minuta* in more elongate, less globular braincase, in longer rostrum that is broader, especially posteriorly, with deeper narial emargination; in longer, wider palate with wider, more substantial bony post-palatal extension; and in larger and more massive teeth. Although in length of forearm the largest of *K. intermedia* overlap the smallest of *K. pellucida,* the ears of *K. intermedia* are smaller, more rounded and like those of *K. minuta,* the skull and teeth smaller than in *K. pellucida,* the braincase much less inflated, the rostrum lower and broader, the palate wider in relation to its length and in particular *K. intermedia* has a broad post-palatal extension that contrasts sharply with the very narrow extension of *K. pellucida.*

Description. Size small (length of forearm (18) 26·7–30·7; in *Kerivoula minuta* (23) 24·8–29·3); ear short for *Kerivoula* (length of ear (18) 9·0–11·4; in *K. minuta* (23) 8·2–9·9), closely similar to ear of *K. minuta*, rounded, funnel-shaped, the anterior margin strongly and evenly convex, rising to blunt, obtuse point; posterior margin of ear with shallow, obtusely angular emargination just below tip, otherwise convex. Tragus long, about three quarters or a little more as long as the ear, its rounded tip about level with the shallow emargination in the posterior margin of the ear, anterior margin of tragus slightly convex proximally, straight for most of its length; posteriorly a prominent tooth-like projection at widest point of tragus, the posterior margin slightly concave above this basal projection. Wing inserted at base of first toe, as in *K. minuta;* as in that species the calcar is long, extending along about two thirds of the uropatagial margin between foot and tail.

Dorsal pelage (from specimens in alcohol) mid-brown, the hairs faintly lustrous, darker basally; ventral surface similarly mid-brown to slightly darker brown, the hairs dark greyish brown at the base and for about one half of their length, otherwise bright paler brown, the basal colour sometimes evident. Proximal part of dorsal surface of uropatagium and dorsal surface of tibiae with a sprinkling of long, golden brown hairs, the ventral uropatagial surface with a few shorter, similarly coloured hairs; uropatagium lacking any marginal fringe.

As in *Kerivoula minuta* the skull is small, short and wide, although the braincase and to a lesser extent the rostrum are more elongate than in that species; braincase slightly inflated posteriorly, slightly elongate anteriorly; rostrum low and broad, posteriorly slightly inflated but not expanded anteriorly; anterior narial emargination narrow, deep, U-shaped, rounded posteriorly; a very shallow median sulcus; zygomata strong and quite massive, lacking any jugal projection; palate long, narrowed anteriorly, widened at level of posterior upper premolars (pm$^{4-4}$), with broad bony post-palatal extension and wide mesopterygoid fossa; shallow basioccipital pits; width of cochleae about one and one half times their distance apart.

Inner upper incisor (i^2) with strong principal cusp and a well developed posterior supplementary cusp extending for about one half the height of the main cusp; outer upper incisor (i^3) a little greater in base area than i^2 and three quarters its height, its tip slightly exceeding the posterior supplementary cusp of that tooth, with well developed cingulum but no cingulum cusps, scarcely separated from the canine; as in *Kerivoula minuta* the first and second lower incisors (i$_{1-2}$) lie more or less along the line of the toothrow, which is strongly arched forward, but the third tooth (i$_3$) lies slightly transversely to it; i$_{1-2}$ tricuspid, i$_3$ a little more massive, with small antero-internal cusp but insignificant postero-external cusp. Anterior premolars (pm$\frac{2}{2}$) more or less circular in outline, the longitudinal diameter of pm^2 very slightly less than its transverse diameter, these about equal in pm$_2$; longitudinal diameters of second premolars (pm$\frac{3}{3}$) and posterior premolars (pm$\frac{4}{4}$) slightly exceeding their transverse diameters; crown area of pm^3 very slightly exceeding that of pm^2, that of pm$_3$ and pm$_2$ about equal; upper premolars slightly compressed in toothrow, the lower premolars less so; lingual margins of m^1 and m^2 rounded, the teeth separated by a wide embrasure.

Measurements appear in Table 4.

ETYMOLOGY. The name selected for this new species reflects the size of its skull, which lies between that of the very small *Kerivoula minuta* and the larger *K. pellucida.*

DISCUSSION. Malayan specimens of this new species have been in the collections of the British Museum (Natural History) for some years. However, there were at the same time no more than three Malayan examples in London of the small form here recognized as *Kerivoula minuta* and only one further specimen from Sabah, so that no real evaluation of their differences could properly be made. Further specimens of both groups from Sabah show that two taxa are involved and although some of their differences are subtle they may be clearly distinguished, a point first remarked by one of us (CMF) who found a considerable difference in weight when examining newly collected examples.

Phoniscus atrox Miller, 1905

Phoniscus atrox Miller, 1905 : 230. Vicinity of the Kateman River, eastern Sumatra.

SPECIMENS EXAMINED. ♀ CMF 821106.06 Madai (in alcohol, skull extracted); ♀ BM(NH) 83.77 Sepilok

Table 4 Measurements of *Kerivoula intermedia* and *K. minuta*

	K. intermedia ♂ BM(NH) 83.356 Holotype. Sabah	*K. intermedia*		*K. minuta*	
		♂♂	♀♀	♂♂	♀♀
Length of forearm	27·7	(10) 26·7–29·5	(8) 28·6–30·7	(19) 24·8–28·3	(4) 28·4–29·3
Length of ear	9·8	(10) 9·0–10·4	(8) 9·6–11·4	(19) 8·2–9·7	(4) 9·1–9·9
Greatest length of skull	12·1	(8) 11·8–12·3	(7) 11·8–12·4	(17) 10·7–11·2	(3) 11·2–11·6
Condylobasal length	11·4	(8) 11·1–11·8	(7) 11·3–11·8	(17) 10·0–10·8	(3) 10·7–11·1
Condylocanine length	11·0	(8) 10·8–11·2	(7) 10·9–11·5	(17) 9·0–10·4	(3) 10·3–10·8
Palatal length	6·4	(3) 6·4–6·7	(3) 6·4–6·7	(12) 6·0–6·2	(2) 6·1, 6·4
Palation-anterior palatal emargination	—	(2) 5·5, 5·6	(3) 5·4–5·7	(10) 4·8–5·0	(2) 4·8, 5·3
Width across anterorbital foramina	3·0	(3) 3·0–3·3	(3) 2·9–3·2	(11) 2·4–3·1	(2) 2·5, 2·8
Least interorbital width	2·9	(7) 2·6–2·9	(7) 2·6–2·9	(17) 2·5–2·9	(3) 2·6–2·7
Zygomatic width	7·5	(5) 7·4–7·7	(5) 7·5–8·2	(12) 6·6–7·0	(3) 7·3
Width of braincase	5·5	(8) 5·5–5·9	(7) 5·4–5·8	(18) 5·0–5·5	(3) 5·4–5·6
Mastoid width	6·4	(4) 6·4–6·6	(3) 6·4–6·6	(12) 5·9–6·4	(2) 6·2, 6·3
c^1–c^1 (alveoli)	3·0	(4) 2·8–3·1	(7) 2·8–3·2	(19) 2·5–2·9	(3) 2·6–2·7
m^3–m^3	5·0	(7) 4·9–5·1	(7) 4·7–5·3	(18) 4·3–4·8	(3) 4·5–4·8
c–m^3	4·8	(8) 4·6–4·9	(7) 4·6–5·0	(20) 4·1–4·6	(3) 4·3–4·5
Length complete mandible from condyles	8·5	(3) 8·3–8·5	(3) 8·3–8·8	(7) 7·4–7·9	—
Length right ramus from condyle	8·7	(4) 8·5–8·7	(3) 8·5–9·0	(9) 7·7–8·0	(2) 8·1, 8·4
c–m_3	5·2	(4) 5·0–5·2	(3) 5·0–5·3	(13) 4·4–4·8	(2) 4·6, 4·8

(in alcohol, skull extracted); ♂ BM(NH) 83.358 (in alcohol, skull extracted), ♀ CMF 830206.2 (in alcohol) Lumerau; all Sabah.

REMARKS. This species has been known hitherto from southern Thailand, Malaya and Sumatra. Specimens from Borneo agree in most respects with those from Thailand and Malaya but are generally a little smaller. Additionally, the braincase in Bornean examples is slightly more elevated frontally than in those from the mainland, with the frontal profile a little more deeply concave; the palate is slightly narrower, especially posteriorly; the outer upper incisor (i^3) is considerably reduced to a narrow spicule; and the maxillary teeth are rather smaller, particularly the molars.

Measurements of CMF 821106.06, BM(NH) 83.77, 83.358 (including skulls) and CMF 830206.2 (forearm only) (in that order), with those (in parentheses) of three (except where indicated) specimens from the Malayan peninsular: length of forearm 31·6, 32·4, 32·3, 32·5, (32·7–34·2); greatest length of skull 14·3, 14·2, 14·4, (14·5–15·2); condylobasal length 13·2, 12·9, 13·1, (13·1–13·8); condylocanine length 13·0, 12·8, 13·0, (13·0–13·7); palatal length 7·6, 7·7, 7·9, (7·9–8·5); least interorbital width 3·6, 3·6, 3·7, (3·8–4·2); zygomatic width 8·2, —, 8·3, (8·5, 8·7, two only); width of braincase 6·8, 6·6, 6·9, (7·0–7·4); mastoid width 7·2, 7·0, 7·2, (7·3–7·5); c^1–c^1 (alveoli) 3·3, 3·4, 3·4, (3·5–3·7); m^3–m^3 5·0, 5·1, 5·0 (5·3–5·5); c–m^3 5·7, 5·6, 5·7, ((5·9–6·1); length complete mandible from condyles 10·1, —, 10·0 (10·5, 10·6, two only); length right ramus from condyle 10·4, —, 10·4, (10·5–11·0); c–m_3 6·1, 6·1, 6·1, (6·3–6·6).

DISCUSSION. *Phoniscus atrox* appears to have been represented in the literature until now by no more than six specimens: the holotype and one other from the type locality in Sumatra, two from Klong Bang Lai, Patiyu, southern Thailand reported in detail by Kloss (1916) and subsequently examined again by Hill (1965), by a subadult from the Ulu Gombak Forest Reserve in Selangor, Malaya, reported by Medway (1969) and finally by one from the Tekam Forest Reserve, Pahang, Malaya, recorded by Hill (1974*a*) and by Medway (1978). Those reported by Kloss (1916) from southern Thailand and by Hill (1974*a*) and Medway (1978) from Pahang are now in the British Museum (Natural History) (BM(NH) 20.7.3.7–8, 71.1135). A direct comparison of specimens from the Malayan peninsular and examples from Sumatra has yet to be made but following Kloss (1916) peninsular specimens have been referred to *P. atrox* with which apparently they agree in all essential respects. Unfortunately, Miller gave no details of the skull or its dimensions in the original account. It seems likely that adequate material might demonstrate that the Bornean and mainland populations are subspecifically distinct but both need to be compared with specimens from Sumatra before any proper decision can be reached.

The only other record of *Phoniscus* from Borneo is of a specimen of *P. jagorii javanus* (Thomas, 1880) from Riam, Kotawaringin district, central Kalimantan, listed by Tate (1941 : 597) who remarks elsewhere (p. 589) in the same paper that there were two specimens from Borneo in the Archbold Collections. However, H. M. van Deusen (in Medway, 1977) reported that only one of these is from Borneo, as listed by Tate: the other is from Bali, as Tate's list shows.

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Synopsis

The fifteen families recognized by Peters (1945, 1948) as comprising the orders Coraciiformes and Piciformes form the subject of this study, which is presented in four parts. The first summarizes available information on feeding behaviour from fieldwork and the literature. In the second part, which constitutes the main results of the investigation, a detailed account of the anatomy of jaws, tongue and neck is given.

Part three examines the anatomical findings from functional and evolutionary standpoints. Overall skull form is discussed in relation to diet, posture and requirements for vision. Kinetic coupling is achieved either via the postorbital ligament, or by modifications of the quadrate-mandible articulation (*Bucorvus* and *Megalaima*); factors affecting the degree and type of coupling are examined. Bony stops and other safety devices present in the kinetic apparatus are reviewed, and their effectiveness assessed. Functional properties of the desmognathous palate are examined; it is noted that this condition is present in large-billed forms, and in families which regularly beat prey against a perch. A distinctive form of pterygo-palatine articulation is present in the Indicatoridae and Picidae; the need for studies of its ontogeny is pointed out. The lower jaw lacks structural features permitting gape enlargement by bowing the mandibular rami, despite the large food items swallowed by many species; possible reasons for this are discussed. Maintenance of the quadrate-mandible articulation is analysed; a medial brace or a deepened medial quadrate condyle are compared as possible alternative forms of protection in groups consuming large or active animal prey.

M. adductor mandibulae externus is the most complex and variable jaw muscle. A detailed compari-

son of its components is made between the families studied here, and published descriptions for birds of other orders. On this basis, certain features (especially the postorbital lobe, narrow M.a.m.e. ventralis and laterally expanded M.a.m.e. caudalis) are considered primitive; the Phoeniculidae and Picidae show these features particularly well. Simpler architecture of this muscle is considered derived, but there are indications that its condition in most Coraciiformes and the Galbuloidea was derived independently from that seen in other Piciformes. The functional significance of complex vs. simple architecture of the muscle is discussed. M. pseudotemporalis superficialis has a mainly lateral origin in typical Coraciiformes and the Galbuloidea, although the whole muscle is much reduced in some groups, and occasionally absent in the Galbulidae. By contrast, a medial extension of origin is developed in typical Piciformes. M. pseudotemporalis profundus is generally parallel fibred, varying mainly in size. It is absent in many Alcedinidae as a consequence of changes in skull form. M. pterygoideus dorsalis is clearly divided into lateral and medial parts, except in the Upupidae, Phoeniculidae and *Ramphastos.* The functional significance of division, and the relative proportions of the two components are discussed. In several families, M.pter.dors.lat. has attachment to the maxillopalatine, permitting the muscle to exert force on the upper jaw directly, rather than through the palatal complex—a feature previously undescribed in birds. Bipinnate structure of M.pter.dors.lat. in several families may be related to small amplitude jaw movements or to isometric contraction. A slip attached directly to the skull base (retractor palatini) is present in the Upupidae, Phoeniculidae and Bucerotidae, derived from M.pter.dors.med. and vent.med. M.pter.dors.med. is divided into anterior and posterior portions in the Coraciidae and Leptosomatidae. M. protractor is much enlarged in the Upupidae, Phoeniculidae and Picidae. In the first two families, this is related to foraging by 'gaping', and is associated with a bulky M. depressor, but in the Picidae, enlargement is a consequence of the muscle's shock absorbing function during hammering, and M. depressor is of normal size.

The tongue is much reduced in the Alcedinidae, Upupidae, Phoeniculidae and Bucerotidae. This may be related to diet in the Alcedinidae, and to bill reinforcement in the Upupidae and Phoeniculidae. Brush tongues occur in several families, showing no obvious correlation with diet or feeding methods. The Picidae show reduction of the tongue itself, but great elongation of the basihyal and hyoid horns to form a probing organ capable of great extension, with a capacity for fine manipulation at the tip. Comparison with other families of typical Piciformes gives some insight into the evolution of this feature. Most Capitonidae, the Ramphastidae and the Indicatoridae possess an entoglossum of distinctive and unusual form.

M. ceratohyoideus is lacking in the Alcedinidae, Indicatoridae and Picidae. M. stylohyoideus, the main tongue retractor, is lost in the Bucerotidae, which rely largely on head jerking to propel food items backward to the oesophagus. It is also absent in the Coraciidae, Galbulidae and Bucconidae, where it is functionally replaced by a slip from M. serpihyoideus; in *Leptosomus*, both this slip and an M. stylohyoideus are present. M. branchiomandibularis ranges from very highly developed in the Picidae to virtually absent in the Alcedinidae. Its sites of origin vary extensively among the Coraciiformes, and may be related to the history of the sporadically distributed M. genioglossus. M. ceratoglossus anterior and M. hypoglossus medialis are best developed in the Meropidae and Galbulidae. M. hypoglossus obliquus is considerably elongated in the Upupidae, Phoeniculidae and typical Piciformes; contracting synergically with M. ceratoglossus, this imparts rigidity to the tongue/basihyal unit during forceful probing actions. Extreme development of this condition is seen in the Picidae, with some approach in the Indicatoridae. M. tracheohyoideus originates either on the clavicle (Coraciiformes and Galbuloidea) or on the sternum (typical Piciformes). In the Bucerotidae it originates on both: this may be the primitive condition from which the two alternatives are derived.

The cervical vertebrae show reduction or loss of fused ribs in the Bucerotidae and Picidae, and in the former, the first and second vertebrae are fused. A sub-vertebral canal is well developed in the Picidae; though enclosing the carotids, its primary function is probably to provide increased surface for attachment of the highly developed M. longus colli ventralis.

The evolution of neck muscle attachments is discussed; reduction in attachment sites is probably a derived state in most cases, but the possibility that increased numbers of attachments might evolve should perhaps not be discounted. M. biventer cervicis is strikingly enlarged in the Alcedinidae, presumably to maintain posture of the heavy head and bill; the Cerylinae and some Daceloninae possess a transverse aponeurosis between right and left muscles. The muscle is also enlarged in *Jynx* and *Indicator,* but in specialized excavators (Upupidae, Phoeniculidae, other Picidae) it is reduced. M. splenius capitis has additional origin on 3 in *Phoeniculus* and some Bucerotidae. M. longus colli is highly specialized in the Picidae, with short slips eliminated and long ones enlarged, enabling the neck to be held rigidly flexed during hammering. M. complexus is highly developed in the Alcedinidae, with origin as far back as 8 or 9 in some; the mechanics and adaptive significance of this are discussed.

M. rectus capitis lateralis is unusually small in the Galbuloidea, where its role may be partly taken over by M. splenius capitis.

In the fourth and final part of the paper, the principal features of feeding apparatus structure are summarized family by family, and their adaptive and taxonomic significance are discussed. The concluding section examines the picture of phylogeny which emerges for the assemblage as a whole. Three main phylectic lines are envisaged; the first consists of the first six Coraciiform families of Peters (1945) together with the Galbuloidea. This line is itself split between the Alcedinidae, Todidae, Momotidae and Meropidae on the one hand, and the Coraciidae, Leptosomatidae, Galbulidae and Bucconidae on the other. The Upupidae, Phoeniculidae and Bucerotidae are considered to represent a second major line, in which the first two families are more closely allied, while the third line consists of the four remaining Piciform families. Among these, the Indicatoridae and Picidae are closely allied, with *Jynx* occupying a somewhat uncertain position between the two. The Ramphastidae are considered directly derived from the Capitonidae. In the classification proposed on the basis of this phylogeny, the Brachypteraciinae and Jynginae are given family rank. The Ramphastidae are, for the present, retained as a family.

Introduction

The avian orders Coraciiformes and Piciformes, as defined by Peters (1945, 1948) comprise 15 families of mainly small to medium sized birds, remarkable for their morphological diversity. This diversity is nowhere more clearly shown than in the structure of the feeding apparatus, so that they form an ideal subject for studies of feeding adaptations and functional anatomy. Curiously, though, relatively scant attention has been paid to these matters, except in the case of the Picidae. Probably, this is because questions of pure taxonomy have always been uppermost, for although some alliance between the two orders has long been generally accepted, the interrelationships of their component groups have never been satisfactorily clarified. The study presented here has concentrated on the adaptive aspects hitherto neglected, but at the same time, has furnished extensive new evidence relating to the evolution and affinities of the various families.

A detailed historical review of the classification has been given by Sibley & Ahlquist (1972), and need not be repeated here. However, some resumé of the present state of knowledge is necessary, and can be conveniently grouped under the headings of three possible types of relationship.

1. Relationships between families within an order. More problems are presented by the Coraciiformes, which fall roughly into three groups. Most heterogeneous of these is that made up by the Alcedinidae, Todidae, Momotidae and Meropidae, which in most respects show only a loose affinity, but share a distinctive stapes form (Feduccia, 1977, 1980). The Coraciidae (including the Brachypteraciinae, treated as a family by some authors) seem fairly definitely allied to the Leptosomatidae (see Cracraft, 1971), but both appear rather distantly related to the preceding families. The Upupidae, Phoeniculidae and Bucerotidae are usually considered to be allied, but the connection between these three and the rest of the order seems less obvious.

Within the Piciformes, relationship between four of the families (Capitonidae, Indicatoridae, Ramphastidae and Picidae) seems fairly well established, but the position of the Galbuloidea (Galbulidae and Bucconidae) is more open to question (but see Steinbacher, 1937).

2. Relationships between Coraciiform and Piciform families. Sibley & Ahlquist (1972) have produced biochemical evidence for affinity between the Galbuloidea and Alcedinidae, and in view of the uncertain position of the former relative to the rest of the Piciformes, the possibility of a connection with the Coraciiformes must be taken seriously.

3. Relationships with other orders. Many such have been proposed in the past, but only three seem at present to merit further investigation. These are, the possible connections between the Indicatoridae and the Cuculiformes (Sibley & Ahlquist, 1972), between the Trogoniformes and the Coraciiformes (Sibley & Ahlquist, 1972; Feduccia, 1977) and between the Piciformes and the Passeriformes. To keep this study within practical limits, only members of the Coraciiformes and Piciformes have been included. However, the findings presented here have some relevance to two of these suggested relationships, arguing strongly against any honeyguide—cuckoo connection (p. 433), but providing tentative support for associating the trogons with the Coraciiformes (p. 437).

The first two parts of this paper are factual, and the following two interpretative. A survey of available information on feeding behaviour is followed by the detailed descriptive anatomy which constitutes the main results of the investigation. In the third part, the anatomical systems studied are re-examined from a functional and evolutionary perspective, and in the final part, the families are reviewed in turn, considering both adaptive and taxonomic aspects. The concluding discussion deals with the principal taxonomic problems, and presents a phylogeny and classification based on the results of the study. The taxonomic nomenclature and classification used is that of Peters, but a problem exists in regard to the naming of structures. This manuscript was already largely complete when the Nomina Anatomica Avium (Baumel, *et al.*, 1979) appeared, and not all the anatomical names used were in agreement with it. The revision needed to achieve total agreement with the N.A.A. would have been a daunting proposition, but it is hoped that the lesser adjustment which has been adopted will suffice. This is to give the N.A.A. equivalent in brackets following all headings in Part 3 which use a superseded term.

Material examined

The anatomical specimens that were available for this investigation are mostly those listed by Blandamer & Burton (1979); the main addition to the orders studied since this list was published is a specimen of *Bombylonax breweri* (Meropidae) presented by Dr C. H. Fry. At least one specimen of every genus in the alcoholic collection has been dissected, and several species in the case of large genera such as *Halcyon*; skeletons of all available genera have also been examined. Four species absent from the collections of the British Museum (Natural History) were loaned by the American Museum of Natural History; these were *Galbula tombacea, Brachygalba lugubris* (Galbulidae); *Nystalus maculatus* and *Hypnelus bicinctus* (Bucconidae).

Birds of several other orders have been dissected to check specific points, and these are noted in the text.

Abbreviations

Jaw muscles, figs 7–24

amec	M. adductor mandibulae externus caudalis
amer	M. adductor mandibulae externus rostralis
amerl	M. adductor mandibulae externus rostralis lateralis
amerm	M. adductor mandibulae externus rostralis medialis
amerp	M. adductor mandibulae externus rostralis, postorbital slip
amert	M. adductor mandibulae externus rostralis temporalis
amev	M. adductor mandibulae externus ventralis
amevc	shared fibres of M. adductor mandibulae externus ventralis and caudalis
ap	M. adductor posterior (N.A.A.: M. adductor mandibulae caudalis)
dm	M. depressor mandibulae
pr	M. protractor pterygoidei et quadrati
pr1	M. protractor, part 1
pr2	M. protractor, part 2
psp	M. pseudotemporalis profundus
pss	M. pseudotemporalis superficialis
pssl	M. pseudotemporalis superficialis, lateral part
pssm	M. pseudotemporalis superficialis, medial part

ptd	M. pterygoideus dorsalis
ptdl	M. pterygoideus dorsalis lateralis
ptdm	M. pterygoideus dorsalis medialis
ptdmp	M. pterygoideus dorsalis medialis posterior
ptmxp	M. pterygoideus dorsalis, maxillopalatine slip
ptv	M. pterygoideus ventralis
ptvl	M. pterygoideus ventralis lateralis
ptvle	venter externus of M. pterygoideus ventralis lateralis
ptvm	M. pterygoideus ventralis medialis
ptvms	medial slip of M. pterygoideus ventralis medialis
qml	Lig. quadrato-mandibulare
rp	retractor palatini portion of M. pterygoideus dorsalis medialis

Hyoid skeleton figs 25–26

bas	basihyal (N.A.A.: basibranchiale rostrale)
cebr	ceratobranchiale
ent	entoglossum
epbr	epibranchiale
uro	urohyal (N.A.A.: basibranchiale caudale)

Tongue muscles figs 27–30

bmd	M. branchiomandibularis
bmdl	M. branchiomandibularis, lateral origin
bmdm	M. branchiomandibularis, medial origin
cgl	M. ceratoglossus
cglap	aponeurosis of M. ceratoglossus
chy	M. ceratohyoideus (N.A.A.: M. interceratobranchialis)
hyp	M. hypoglossus obliquus
mhy	M. mylohyoideus (N.A.A.: M. intermandibularis)
sehy	M. serpihyoideus
sehya	M. serpihyoideus, anterior slip
sthy	M. stylohyoideus
thy	M. thyrohyoideus (N.A.A.: M. cricohyoideus)
thyd	M. thyrohyoideus, dorsal part
thyv	M. thyrohyoideus, ventral part
trhy	M. tracheohyoideus (N.A.A. nomenclature: see text)

Cervical muscles fig. 31

asc	Mm. ascendentes cervicis (N.A.A.: M. cervicalis ascendens)
co 6–8	M. complexus, slips of origin from vertebrae 6 to 8
itr	M. intertransversarius
rcs	M. rectus capitis superior (N.A.A.: M. rectus capitis dorsalis)
spin	M. spinalis cervicis (N.A.A.: M. longus colli dorsalis)
spla	Mm. splenii accesorii
splc	M. splenius capitis

PART 1

Feeding behaviour

This section presents a digest of available information on feeding behaviour in each family, derived largely from a survey of the literature, but also to some extent from personal observations carried out in the course of this study. Some of the latter have already been published at greater length elsewhere (e.g. Burton, 1977, 1979), while others are in preparation. The account given here concentrates mainly on the actions performed by jaws, tongue and neck during feeding. Details of diet and some general ecological background are given, but to pursue these aspects further, it will be necessary to consult the references given.

ALCEDINIDAE

Despite their name, most kingfishers do not fish. Of the three sub-families, only the Cerylinae is exclusively piscivorous. The Alcedininae also hunt mainly by plunge diving, though in several species (e.g. *Alcedo leucogaster, A. cristata, A. meninting*), it appears that the prey is aquatic insects and other organisms rather than exclusively fish. Some (e.g. *Ceyx* spp.) apparently eat mainly terrestrial or aerial insects. The Daceloninae are predominantly terrestrial feeders, and only a few, notably *Pelargopsis* spp. hunt regularly by plunge diving. Unfortunately, precise information is lacking on the feeding behaviour of most members of this large and diverse subfamily, even such specialized forms as the nocturnal *Melidora,* or *Clytoceyx* which apparently excavates mud for worms with its short but massive bill. Further details on feeding habits throughout the Alcedinidae are provided in the review by Fry (1980).

Whether the prey taken are aquatic or terrestrial, the feeding strategy employed is essentially the same throughout the family; a likely area is scanned from a perch, and periodically a sally is made to capture prey. Searching and sallying are nearly always directed downward to prey on the ground or in the water. A few kingfishers show more versatility; *Halcyon pileata,* for instance, seeks prey with frequent head movements directed to foliage above as well as below (Burton, 1979). Several species capture airborne insects, e.g. *Ceyx* spp., even *H. chloris* (Burton, 1979). Aquatic prey may be sought in hovering flight, particularly among the Cerylinae, notably *C. rudis* (Douthwaite, 1976).

Prey captured are usually large relative to the size of the bird, including reptiles, nestling birds and small rodents in the case of the larger Daceloninae. Capture rates are fairly low, particularly in large species. Prey are commonly beaten against the perch before consumption, with a sharp sideways action. *Dacelo novaeguineae* drops snakes to the ground repeatedly to kill them, and there are records of two individuals cooperating to kill a snake (Keast, 1969). There is some evidence that scorpions may have the sting removed before consumption (Burton 1979, *H. concreta*), but details on the treatment of venomous prey are generally lacking. Fish are swallowed head first, after being oriented along the bill axis. For *A. atthis,* many photographs exist showing fish grasped in the bill (those with the head forward are probably destined for nestlings). In at least some, e.g. Massny (1977), the jaws appear almost parallel, with the lower projecting slightly beyond the upper, evidence of strong retraction of the upper jaw.

Plunge diving, ideally, is accomplished by an almost vertical drop from the perch. However, in species which fish from perches, many dives are strongly oblique. The author has seen *A. atthis* make captures after a slanting flight of nearly 10 metres from a low perch; such instances imply considerable skill in compensating for refraction. There is presumably some relation between the height of dives, and the depth of penetration into the water, though this relationship is unlikely to be a simple one due to habits of prey and availability of perches. However, larger species tend to dive from greater heights than smaller ones, and presumably thus have access to deeper swimming fish. In *A. atthis,* at least, the nictitating membranes cover the eyes on entry to the water, and if the fish evades capture, inanimate objects may be briefly grasped, suggesting that the prey cannot be seen during the final moments of the attack. The bill is held slightly open as the water is entered (see Junge & Lutken, 1974).

An important use of the bill in all the Alcedinidae is nest excavation. Usually the nest burrow is excavated in a bank of sand or earth. The process has been well described by Eastman (1969). The tunnel is started by flying at the bank and striking it with the bill. Once enough material has been removed to gain a purchase with the feet, excavation continues from a perched position, until the bird is far inside the tunnel, working with the bill, and using the feet to shovel out material. Some kingfishers at least occasionally excavate wood. Excavation of a tree nest site by *H. chloris* has been described in detail by Harrisson (In Smythies, 1960) and England (pers. comm.) kept a pair of captive Kookaburras, *Dacelo gigas*, which cut through an inch thick board of elm wood. The writer has found a nest of *Ceyx pusillus* in the trunk of a rotten tree in lowland rainforest in New Guinea.

TODIDAE

The feeding behaviour and ecology of the todies have been described in great detail by Kepler (1977) from whose paper this account is condensed. Todies forage in a variety of brush or forest habitats, favouring situations with an abundance of twigs, branches and leaves. Insects are captured from all available substrates; in descending order of preference these are leaves, twigs and branches, the air, inflorescences and fruits, and the ground. Perches chosen are those not normally covered by close-touching leaves, and affording a view both above and below. Foraging heights for most species are generally substantially below canopy level; *T. subulatus* forages higher than *T. angustirostris,* and this difference is most marked where both occur together.

Kepler describes two principal feeding methods and three minor ones. Most frequent of all is leaf feeding; the bird perches with bill inclined upwards at angles up to 45° from the horizontal, and scans the undersides of leaves and twigs above it. Seeing an insect, it flies up to the leaf or twig, snaps its bill, and continues in an unbroken arc to another perch. Occasionally insects are taken from the tops of leaves in a downward swoop. Air feeding, second in importance, consists of flycatcher like sallies to capture a passing insect, usually returning to a different perch. Minor feeding methods are hovering in front of feeding substrates, snapping prey from tree trunks, and sliding along perches to glean prey in warbler fashion. After a capture, the insect is usually swallowed in flight, but they kill larger ones either by flicking their heads to and fro or by vigorous beating against twigs for up to a minute.

Feeding rates are greatest in xeric scrub, averaging 1·7 per minute, and slowest in rainforest, averaging 1·0 per minute. Capture rate averages about 41% in dry scrub and 33% in rainforest. Flight distances range from about 1·9 m to 2·6 m., varying somewhat according to species and habitat. Where *T. subulatus* and *T. angustirostris* occur together, the former flies longer distances, illustrating another feature of their behavioural divergence.

Prey recorded for *T. mexicanus* includes 11 insect orders, spiders, and small amounts of miscellaneous items, including plant material. Diptera account for about 31% of the adult diet, and Coleoptera for 23%. Food given to nestlings includes much fewer Diptera, but considerably more Momoptera and Lepidoptera.

The bills are also used for excavating nest tunnels in banks, and occasionally in rotten wood. Sometimes several centimetres of mosses and liverworts have to be torn away to expose the soil. The burrows are usually curved, and Kepler records an average length of 30.5 cm in wet forests, slightly shorter (26·9 cm) in dry scrub. Excavation usually lasts several weeks, the tunnel growing at about 0·5 cm per day. When starting a tunnel, the birds hover in front of the bank, jabbing it with their bills in bouts of 2–5 thrusts. Loose debris is scraped out with the feet, though occasionally large particles may be carried out in the bill.

MOMOTIDAE

Baryphthengus spp. are generally birds of the middle to lower stories of the forest, feeding on large animal prey with some fruits. Johnson (1954) noted *B. martii* in attendance near ant swarms, perching quietly watching for prey animals moving out to escape the ants; these were then taken from tree trunks or palm leaves. One bird which took a large scorpion spent five minutes killing the creature before swallowing it whole; Johnson's account does not mention treatment of the sting. Small lizards, orthoptera, caterpillars, wasps and various fruits are other food items recorded by Wetmore (1968) for *B. martii.*

Closely similar to *Baryphthengus* in diet and habits, *Momotus* spp. range into relatively open areas of second growth or into isolated thickets, as well as forest. Wetmore (1968) and Skutch (1964) record that small birds are exceptionally taken as prey; other items recorded are similar to those listed for *B. martii.* Prey are banged on the perch vigorously and repeatedly, either to quieten them, or to break off wings. Skutch (1964) notes for *M. momota* that seeds of the nutmeg family are swallowed whole, to digest the thin aril surrounding the seed, which is later cast up intact. Though most hunting seems to be done by watching from a perch, *M. momota* may be seen to forage for extended periods on the ground, hopping about with tail cocked up in a manner reminiscent of a thrasher, *Toxostoma.* Skutch (1964) noted an individual of *M. momota* on the ground, apparently searching for a dropped prey item, pushing aside fallen leaves with alternate sweeps of the bill to left and right.

Hylomanes is the least known genus of the family. Wetmore (1968) says it is found alone or in pairs, resting quietly in open undergrowth in humid forest. Prey recorded by him include a spider, a snail, Coleopter, Orthoptera, Homoptera, caterpillars and ants.

Motmots also use their bills to excavate long burrows in earth banks for nesting. An account of excavation in *M. momota* is given by Skutch (1964).

MEROPIDAE

The most thorough survey of Bee-eater feeding behaviour is contained in a comparative study of the various African species by Fry (1972). Except for Asian and Australasian Meropidae, the details which follow are condensed from his account, with extensive verbatim passages.

Small bee-eaters, such as *M. pusillus, M. variegatus, M. orientalis,* M. boehmi and *M. reviolii* feed by 'fly-catching'. They keep watch for flying insects from low perches, usually within 2 metres of the ground, and make brief sorties of seldom more than a few metres, returning to the perch with their victim and immobilizing it there. Like all bee-eaters, they are extremely adept at catching the prey, which seldom escapes.

Middle size *Merops—M. hirundineus, M. oreobates, M. bulocki, M. bullockoides, M. albicollis* and *M. gularis*–also behave like flycatchers, returning to the perch to beat their prey. But they select more elevated vantage points, fly farther after insects, and range more widely, foraging during the course of a day over hundreds of acres or along as much as a mile of wooded watercourses. Upon alighting these species swallow small insects, for example the 5 mm long, stingless 'sweat-bees' (*Trigona* spp.) without treatment, but they immobilize larger insects before eating them. Among *M. bulocki*, the mean of 66 counts of feeding flights, made in and out of the breeding season in all weathers, was 5·2 sorties every 10 minutes. Since these birds average 11 waking hours a day in active feeding and make very few sorties without a capture, an individual *M. bulocki* must eat about 340 insects a day or 124,000 insects a year.

Large birds such as *M. superciliosus, M. malimbicus, M. apiaster* and *M. nubicus* tend to use tree top perches and to range even more widely, over a few square miles daily. They are also more prone to hunt in continuous flight. *M. apiaster* may be seen twisting and wheeling in flight high over the savannas, catching probably soft-bodied insects such as flying ants and termites. With a large and hard bodied insect, they must return to a perch to immobilize it by beating and if necessary, devenoming it before eating it. (Fry, 1969).

The two species of *Nyctiornis* are less aerial than the smaller bee-eaters. The habits of

N. athertoni are summarized by Smythies (1953); much of its food is obtained while clambering about in trees, taking insects directly from leaves or flowers. Prey include various large insects, such as beetles, in addition to bees. *N. amicta* is more strictly a forest bird, preferring areas where trees are more thinly spaced, especially near the edge of streams or swamps. (Smythies, 1953, 1960; Robinson, 1928). Found in pairs or small groups, it perches at a height of 3 to 6 metres, darting out occasionally to seize prey; it will also clamber about in trees at times like *N. athertoni.* Its flight is noticeably less swift and more laboured than the smaller bee-eaters.

Bee-eaters nest in burrows excavated in cliffs or flat ground. Soil is loosened with the bill and kicked out with the feet; Fry (1972) observes that they will often support the body on a tripod of bill and carpal joints, enabling both feet to be used together. He also notes that a frequent cause of death in all species is getting the head and bill jammed sideways in the tunnel.

LEPTOSOMATIDAE

The little we know of the feeding habits of *Leptosomus* is largely contained in the accounts by Rand (1964), Forbes-Watson (1967) and Appert (1968*a*). The Cuckoo-roller inhabits forest and brushland, where it stays largely in the tree tops, and is often seen in small parties. According to Rand (1964), the food consists of chameleons, locusts, caterpillars and other large insects. The stomach is often lined with hairs from caterpillars. Large caterpillars, and probably other prey, are held in the bill and beaten against a perch to subdue them before being swallowed.

Forbes-Watson (1967), who watched a nest of *Leptosomus discolor* found that the two young were each being fed six chameleons per day during the period of his observations. He comments that there must either be considerably more chameleons than one would suspect, or the birds must have a large hunting territory and be extremely efficient at finding chameleons. Neither Rand (1964, 1936), Benson (1960) or Forbes-Watson (1967) record other lizards as prey, although Forbes-Watson notes that these were abundant and conspicuous on the ground in the vicinity of the nest he watched. Probably most, if not all, the food, is taken above ground-level. Appert's (1968*a*) observations give a similar picture except that at a nest he watched, caterpillars seemed to be the main food brought by the male to the incubating female, and by both sexes to the young.

CORACIIDAE

The rollers fall into three distinct groups as regards way of life and feeding behaviour. Typical rollers, *Coracias,* watch for prey on the ground from an elevated perch, fly to seize it, and then consume it there or return with it to the perch; more rarely, they may catch aerial prey, or forage for some time on the ground. Broad-billed rollers, *Eurystomus,* also watch for their prey from a perch, but feed almost entirely on insects captured in flight. When dense swarms pass by, they may stay on the wing for several minutes, making repeated captures while sailing or dashing about with a buoyant and agile flight action. The ground-rollers, confined to Madagascar, are a distinctive group of genera sometimes separated as a family (Brachypteraciidae). They are entirely ground living, and at least some are believed to be partly nocturnal.

Detailed studies of roller feeding behaviour are lacking, though some quantitative information on foraging in *E. orientalis* will be presented in a forthcoming paper on the Artamidae (Wood Swallows) with which it often associates (Burton, in prep.). A good survey of food and ecology in some West African species is given by Thiollay (1971). *Coracias* spp. had taken Coleoptera, Orthoptera, ants and termites in roughly similar quantities; *E. glaucurus* had consumed winged ants and termites in great numbers, but otherwise, prey was predominantly coleopteran. Termites, coleoptera and cicadas are recorded for *E. orientalis.* Other accounts bear out this general picture, though larger prey (scorpions, lizards, etc.) are often recorded in the case of *Coracias*. Exceptionally, *Eurystomus* has been recorded diving into water to take fish.

Apart from the fact that ground rollers do not normally hunt from perches, prey and feeding methods seem unlikely to differ in essentials from those of *Coracias*. The evidence for their nocturnal habits is partly based on native sources which Rand (1964) considered unreliable, but crepuscular and nocturnal behaviour has been confirmed in *Uratelornis* by Appert (1968*b*).

Coracias, Eurystomus and probably *Brachypteracias* nest in natural cavities, and hence do not use the bill for excavation. However *Uratelornis* certainly excavates a breeding tunnel, and probably also *Atelornis pittoides* (Rand, 1964). The breeding habits of *A. crossleyi* are unknown.

UPUPIDAE

The hoopoe forages principally on the ground, and the following account of its feeding techniques is condensed from the account by Skead (1950). Hoopoes probe assiduously throughout the day, with the bill tip slightly open but not usually penetrating the soil to any great depth in and around grass tussocks. In softer soil the bill may be inserted full length. Prey items are held at the bill tip for a second before being tossed back into the mouth with a short, sharp jerk of the head. Skead once watched a male digging in one spot for five minutes, excavating a hole so deep that his forehead disappeared from view. The prey extracted was pounded heavily on the ground to break it up into pieces small enough to swallow. Hoopoes nearly always probe in short grass rather than long. Probing in wood is rare, but they frequently and successfully probe around the bases of fence posts. Dry cow-pats are flicked over with a deft sideways sweep of the bill, or tipped over backwards. Skead has occasionally seen hoopoes fly up from the ground to hawk flying termites. Prey listed in this and other accounts include a large proportion of insect larvae, especially coleopterous, mole crickets, scorpions and lizards.

PHOENICULIDAE

Unlike the hoopoe, wood-hoopoes virtually never forage on the ground. *Phoeniculus* spp. seek food principally on tree trunks and branches, clambering about over them and probing into crevices and behind loose bark. Prey taken is chiefly insects, including beetles, termites and ants, but small fruits are occasionally eaten. The scimitar bills, *Rhinopomastus* spp., are even more specialized, with a particular fondness for acacias. The behaviour of *R. cyanomelas* is well described by Brown (1969) who writes as follows:

> Normally the bird is seen climbing about in the tops of acacia trees, or clinging to the bark as it works up or down, searching minutely for insects. It then behaves more like a creeper or tit than a wood-hoopoe, sometimes hanging upside-down on a branch, or again probing crannies in the bark with head held downwards. When feeding it constantly probes small holes and cracks delicately and gently, or pushes the bill round under stems and the globose flowers of the acacias. Evidently it survives mostly on very small insects.

Brown goes on to describe how the bird works its way along branches of the ant-gall acacis, *A. drepanolobium,* probing with its fine bill into the tiny openings by which ants enter and leave the galls. Presumably small grubs or pupae are obtained in this way.

BUCEROTIDAE

Tockus spp. are generally fairly small and have less enlarged and elaborate bills than most other hornbills. Their diets are wide, and their feeding methods highly versatile. Kemp (1976) has described these in some detail, and distinguishes the following techniques, which are quoted verbatim:

> 1. Picking—The food item is picked up where it is found in the vegetation or on the ground, while the bird is standing.

2. Digging—Standing on the ground, the bird pushes the closed bill into the substrate and then flicks the dirt to one side, partly opening the bill at the same time. Food items are thus exposed.
3. Levering—On the ground, the head is lowered to one side and the closed bill slid under an object. Raising the head causes the bill to work as a lever to turn over the object. This is used when the object is too large to be moved by the digging action, and exposes the food items underneath.
4. Chasing—Pursuing an active food item on the ground.
5. Swooping—Flying down from a perch to obtain a food item that has been noticed on the ground below.
6. Plucking—Picking up a food item from the ground or vegetation without landing.
7. Hawking—Catching a flying food item whole on the wing.

Less detail is available for other members of the family, but all authors who have watched large hornbills feeding stress the dexterity and delicacy with which the huge bill can be used. For example, Fogden (1969) writing about *Anthracoceros malayanus* describes a technique used for dealing with potentially dangerous prey such as snakes, centipedes or scorpions. The creature is held by the very tip of the bill and repeatedly squeezed throughout its length, working from end to end several times. The extremities are given a particularly vigorous squeeze, ensuring that the head or tail sting are completely crushed. Objects such as twigs and leaves are often manipulated in 'play' in the same way. Similar dexterity is also shown in dealing with fruits, which the birds are capable of peeling using the bill alone. Objects to be swallowed, whether fruit or animal, are swallowed by tossing them into the air with the bill tip, then shifting the head and open bill to catch them at the rear of the buccal cavity.

This picture generally holds good for most hornbills, whether omnivorous or primarily fruit eaters, but a few show additional specializations. Ground hornbills (*Bucorvus*) are adept at finding and excavating for underground wasps' or bees' nests; honey comb is removed and carried away impaled on the bill tip. *Rhinoplax vigil,* with its relatively short bill and heavy solid casque appears to be adapted for wood excavation, though substantiating field observations are scanty at present.

An activity common to most hornbills though not *Bucorvus* is that of plastering mud or excreta around the entrance of the nest cavity to wall in the incubating female, using the sides of the bill to smear or pat material into place.

GALBULIDAE

Jacamars typically forage in flycatcher style, by making aerial sallies from a perch to catch passing insects. The most detailed published account of feeding behaviour is that for *G. dea* by Burton (1977). This species feeds mainly from relatively high perches at the edges of clearings, rather than from the low perches in scrub or forest favoured by most other jacamars. Feeding flights usually commence with a dive from the perch, followed by a swift pursuit, often involving rapid and agile changes of direction. Occasional flights are made directly upwards. After a capture, the bird returns to a perch with an undulating flight; perches were changed after about 50% of the flights. Flight distances ranged from about 1 to 12 metres, mostly from 4½ to 9 metres, and were of short duration—1·3 to 5·6 seconds, averaging 3·2. Only a single capture occurred in all flights observed. Frequency of flights averaged 21·8 per hour over 5 hours, considerably greater than in *Chelidoptera tenebrosa* (Bucconidae) which feeds by aerial sallies in similar habitat to *G. dea,* and is of similar body size. Prey captured were frequently fairly large, including butterflies, dragonflies and sizable wasps. Large prey were sometimes banged on the perch several times, but back and forth rubbing to devenom Hymenoptera has only been recorded once.

Other species of *Galbula,* and probably also *Brachygalba* and *Jacamaralcyon,* show simibehaviour, though as perches are generally lower, upward flights are more frequent, and perched birds generally sit with the bill inclined upwards at about 45° (about 20° in *G. dea*). Activity rates are probably higher in smaller species; the writer's limited observations on *G. galbula* suggest a flight frequency twice that of *G. dea,* and much more rapid head movements while sitting perched, though the length and duration of flights is generally less. As in *G. dea,* prey generally seem to average fairly large for the size of the bird, with Hymenoptera predominating. Also, as Wetmore (1968) points out, jacamars are one of the few groups of birds which regularly catch and eat butterflies.

Jacamerops aurea differs from other jacamars in its more sluggish behaviour. Detailed quantitative observations are difficult to compile for this species, which is usually encountered perched moderately high (6 to 10 metres) at the edge of a small clearing in forest. It may sit motionless for several minutes before making a short sally and returning to a new—and frequently invisible—perch. Usually prey taken in these sallies are seized from foliage rather than in flight.

Galbalcyrhynchus, one of the most distinctive genera of jacamars, is also one of the least well known, though it may be surmised that its exceptionally heavy bill denotes a preference for large or hard bodied prey.

Jacamars excavate nest burrows using the bill usually in earth banks. Skutch (1937, 1963), writing about *G. ruficauda*, notes that the bill is used for loosening particles of earth, which are periodically kicked out with the feet, though occasional small lumps are carried out in the bill. Nests are sometimes found in termitaria, though it has not been proved that these were actually excavated by the jacamars themselves in such a hard material.

BUCCONIDAE

A detailed account of feeding in *Chelidoptera* has been given by Burton (1977). This is the most aerial, and one of the most active of puffbirds, resembling more the Wood Swallows (Artamidae) of the Oriental and Australasian regions in its general behaviour and way of life. Most of its prey are small insects, including many Hymenoptera, captured in flight. Though less frequently using agile manoeuvres to catch prey than most jacamars, its sorties are frequently more prolonged, and may sometimes exceed a minute in length, with several captures interspersed by bouts of soaring. Perches commonly used are dead branches near the tops of trees in clearings or at forest edges, on which small groups of the birds often sit close together. Prey are mostly swallowed in flight, and rubbing or beating against the perch was not observed.

Amongst other puffbirds, *Monasa* shows the closest approach to *Chelidoptera* in feeding behaviour (Skutch 1972; Burton, unpubl.), making frequent aerial sallies, which, however, are usually to seize prey from foliage, tree trunks and branches, or sometimes the ground, and less frequently to capture flying insects. They associate in small parties, usually up to a maximum of six and generally return to a new perch after a feeding sortie, with the effect that the whole group gradually moves in straggling fashion through the forest. Sallies usually involve simply a glide on set wings, occasionally with a brief hover as prey is taken, though they are capable of rapid manoeuvring when necessary. Prey include many cicadas, orthoptera, beetles, dragonflies and occasionally butterflies, and also some spiders and millipedes. In contrast to *Chelidoptera,* larger prey are often beaten or rubbed against the perch, for periods of up to a minute. This is by no means confined to venomous species, but if intended to remove wings and legs is not strikingly successful; I have seen even butterflies swallowed whole after a bout of beating. A curious item of behaviour noted by Skutch is the feeding of adult birds by other members of the foraging group.

Nonnula spp. are small members of the family which glean insects off foliage from undergrowth to lower tree crowns, often moving actively through cover as they forage, but sometimes waiting for a time on a perch like other puffbirds. Wetmore (1968) records orthoptera, caterpillars, earwigs, small beetles, membracids and spiders from stomachs. Equally diminutive, *Micromonacha lanceolata* may be similar in habits, though no information is available.

Most other members of the family are larger, more heavily built birds which somewhat resemble forest kingfishers of the genus *Halcyon* in their habits. Normal foraging strategy is to sit on a tree perch at moderate height, motionless but for regular head movements, often waiting for many minutes until prey is seen. After a short flight to seize this, the bird returns to the same or another perch. Prey taken are usually large insects, obtained mostly from branches or leaves, though *Bucco* spp. perhaps take more from the ground or low herbage.

Puffbirds nest in burrows excavated in earth, or occasionally termitaria. The process of excavation has been observed only in *Notharcus pectoralis* (Skutch, 1948), working on a termitarium. Although this pair were invisible when inside the chamber, Skutch judged from sounds that material was removed by biting or tearing, as well as by hammering. He also notes that in three other species, *Malacoptila panamensis* (Skutch, 1958), *Monasa morphoeus* (Skutch, 1972) and *Chelidoptera tenebrosa* (Skutch, 1948), no excavated earth is found around the burrow entrance, suggesting that this is carried away by the birds. Sticks and dead leaves are placed around the entrance by these three species, a habit especially strongly developed in *Monasa.*

CAPITONIDAE

Barbets occupy a variety of tropical habitats ranging from rainforest to acacia savannahs and dry scrubland. The diet of most species appears to be primarily fruit with some insects, but because of the difficulties of observation in many of their habitats, information on feeding techniques is derived largely from captive birds (See especially England, 1973*a* & *b*, 1975, 1976, 1977).

In the wild, the numerous species of figs are probably a major food source for many forest barbets. An interesting photograph in Thomson (1964) shows an individual of *Megalaima zeylanica* carrying four figs simultaneously in its bill. In more open or arid habitats, various berries are recorded, as well as leaves and shoots. Tinker-barbets, *Pogoniulus* spp., often use the berries of mistletoes as a staple item of diet. Insect items recorded include many Orthoptera, as well as beetles, ants, etc. Termites are probably important to *Trachyphonus* spp., at least one species of which nests in termite mounds.

Captive barbets subsist satisfactorily on a variety of prepared fruits, but England notes for several species that the diet switches largely to insects just before and during breeding. It appears that the young are fed mainly on insects at least until the later stages of fledging, as Skutch (1944) observed for *Semnornis frantzii* in the wild. Under aviary conditions, mealworms and locusts are the principal insect food supplied, and their treatment by the barbets is of some interest. Mealworms are often 'mandibulated', that is, crushed and softened by running them from one end to the other several times through the bill tip, which makes many rapid small amplitude bites on the insect. This process is used especially, though not exclusively, when the mealworm is to be fed to fledglings.

Treatment of locusts varies from one species to another. Thus, England (1975) notes that *Eubucco bourcieri* holds the victim on the perch by one foot, or sometimes both, and very occasionally raises a foot to the beak, usually to remove and clasp food which requires more tearing up before swallowing; *Trachyphonus erythrocephalus* holds the locust in its bill by a leg or a wing and shakes it violently until the body comes off, repeating the process until it is devoid of appendages; *Megalaima chrysopogon* seizes and mandibulates the locust, occasionally throwing it up to catch it another way round, then finally swallows it whole. The writer watched *M. zeylanica* and *Psilopogon pyrrholophus* both confronted with a locust for the first time; *M. zeylanica* treated the insect exactly as did England's *M. chrysopogon,* while *P. pyrrholophus* appeared nonplussed, and after a few desultory attacks finally ignored it. More interestingly, a captive specimen of *Semnornis rhamphastinus* treated the locust in a similar way to England's *Eubucco,* using a foot to hold it on the perch. The extraordinary pronged bill tip was then used with great dexterity to systematically pluck all appendages off the locust's body, attacking them near the base, where they were attached to the thorax. The insect was then consumed without further treatment.

Use of the feet has been noted also in *S. frantzii* (Skutch, 1944), which apparently is mainly vegetarian in the wild, consuming fruits, berries and the petals of flowers. Skutch notes that by contrast, *E. bourcieri* in the Costa Rican forests is insectivorous, spending its time well up among forest trees, where it investigates curled or rolled dead leaves, either probing the interior, or biting them on the outside to drive out prey. The Asian *Calorhamphus fuliginosus* appears to have similar habits, foraging in small parties, and investigating crevices and crannies of all kinds, often behaving in an acrobatic manner more reminiscent of a tit than a barbet (Hume & Davison, 1878). *Megalaima haemacephala* is recorded as making ungainly aerial sallies after insects (Hyatt, in Gooders, 1969–71).

Most barbets use their bills for nest excavation, as well as for feeding. In the great majority, nest holes are bored in rotten timber, even colonially in at least one genus (*Gymnobucco*). *Trachyphonus* spp. excavate in banks, termite mounds, or the ground. The form of the nest chamber and its entrance varies, but it is generally more irregular than those of woodpeckers (Picidae). An account of excavation techniques given for *Tricholaema diadematum* by England (1973*a*) is probably fairly typical. He writes '. . . each would attack the wood, hammering away until a piece was loosened at one end; this was then seized and torn off and, when a large beakful was free, it was carried to the far end of the flight and dropped onto an ever-increasing heap. Amazingly, small pieces of wood were swallowed and *regurgitated* on to the heap; practically nothing remained beneath the hole to give the site away to enemies.' Similar techniques have been observed under natural conditions for *Semnornis frantzii* by Skutch (1944). Use of the bill in grasping or consuming wood, and the habit of carrying debris away are important differences from the excavation methods of woodpeckers. Excavation continues during the fledging period as noted by England and by Skutch (1944). The debris thus produced serves the function of soaking up the nestlings' droppings, and soiled wood chips are regularly carried away. In general, the nesting habits of barbets appear more varied and flexible than those of woodpeckers, even if their architecture is less perfect. Fuller details of their interesting breeding biology are given by Skutch, and in the series of papers by England.

INDICATORIDAE

The honeyguides are remarkable for their ability to use wax as a food source (see Friedmann, 1955 for a full account). In the case of the genera *Indicator, Melichneutes* and *Melignomon* this is derived from the combs of wild bees; the bees themselves, and their larvae and pupae are also eaten. At least two species of *Indicator,* both African, have evolved a relationship with ratels and men in which these predators are guided to the bees' nests by the birds, which can then feed with ease on the remains of the nests after they have been plundered. This is by no means the only food source of honeyguides; a variety of insects are eaten, often captured on the wing.

The smaller sharp-billed Honeyguides (genus *Prodotiscus*) do not attack bees' nests, but nevertheless obtain a considerable amount of wax by eating scale insects (Hemiptera, Homoptera, Coccoidea).

Honeyguides are parasitic in their nesting habits, and the nestlings of at least two species of *Indicator* possess well developed hooks at the tips of both jaws which are used to bite the young of the host, eventually causing death; a detailed account of this behaviour in *I. minor* is given by Friedmann (1955). The hooks are lost early in the fledging period. It is not known whether *Prodotiscus* spp. behave similarly, or possess such hooks, although Maclean (1971) found none in a week old *P. regulus.*

RAMPHASTIDAE

Toucans are primarily fruit eaters, but also take a variety of small animals, including insects, reptiles, and the eggs and nestlings of other birds. Fruits are plucked with the mandible tips, then tossed back with an upward jerk of the head. Despite its size, the bill can be used with some precision, as when birds pass food from one to another. Skutch (1972) suggests for *R. swainsonii* that the size and colours of the bill have an intimidatory value, useful when nest robbing. He also notes that toucans are unable to turn the head back in flight for self defence, a fact which small birds take advantage of when mobbing them. Skutch mentions two

Swainson's Toucans with severely broken bills which nevertheless survived in the wild for at least 2½ years and 7 weeks respectively.

Feeding behaviour is essentially similar in the smaller toucans such as *Aulacorhynchus* spp., and Skutch (1967) has provided a description of nest excavation by *A. caeruleogularis*. Rotten wood was the chosen substrate, and was excavated by pecking and hammering, blows being often (perhaps always) delivered with the jaw tips slightly parted. Only the foreparts were moved when delivering blows, not the whole body. The birds also seemed to bite away pieces of rotten wood. Large billfuls of excavated material were removed at intervals and carried some distance away as in many barbets.

No unusual function in feeding has been ascribed to the exceptionally well developed tongue, although several observers, the writer included, have made a point of looking out for some special form of tongue action.

PICIDAE

The Jynginae (wrynecks) do not excavate, either for food or to make nest holes, but rely entirely on the long protrusible tongue to take food, either from the surface, or from tunnels and crevices. Ants make up a large proportion of the diet of small insects. Though neck movements while feeding appear unremarkable, both threat and courtship displays involve extraordinary contortions of the neck.

Piculets (Picumninae) principally exploit fine twigs, vines, leaf petioles, etc., hammering them in typical woodpecker fashion to gain access to ants and grubs. The tail is not used to prop the body while hammering as in woodpeckers. A good general account of foraging by *Picumnus olivaceus* is given by Skutch (1969). He also quotes Miller (1947) who notes that in Columbia this species shows great versatility, including nuthatch like behaviour in which the bird moves down tree trunks head first. *Sasia* spp. show a fondness for fallen tree trunks and logs, as well as for fine twigs and bamboo. *Verreauxia* evidently forages in a generally similar way to other piculets, but is said to prefer grubs to ants (Bannerman, 1951). All piculets excavate their own nest holes either in trees or bamboo.

Woodpeckers (Picinae) make up the largest of the three subfamilies. They subsist typically on a diet of wood and bark-boring insects, but some, especially *Melanerpes lewis* and *M. formicivorus,* take aerial insects, and other foods include acorns and other nuts, and even cambium and sap, obtained by boring holes through bark (*Sphyrapicus* spp.). The bill is used not only for feeding, but also for nest excavation and to produce 'drumming'—an instrumental sound with territorial significance. An excellent account of both these activities is given by Sielmann (1958). The feeding process also involves sophisticated techniques using the highly modified and protrusible tongue.

A detailed account of woodpecker feeding methods has been given by Spring (1965); an important earlier study was made by Burt (1930). Spring concentrated on three species—*Sphyrapicus varius, Dendrocopos villosus* and *Picoides arcticus.* He described the action of hammering carefully, and used ciné photography to assess the contribution of body and neck to the blows. The contribution of the neck was greatest in *Sphyrapicus,* which holds its body closer to the trunk than the other two species; it consequently strikes less powerful blows, but since most of its food is obtained near the surface, deep excavation is not needed. Spring notes that leg and foot adaptations enabling the body to be held well off the trunk impose a penalty of decreased climbing efficiency in the species he studied, but he could not demonstrate any difference in blow delivery between *D. villosus* and *D. pubescens*, or between *P. arcticus* and *P. tridactylus,* despite some anatomical differences. Personal observations of a wide range of woodpeckers seem to indicate that a substantial part of the force of hammering is provided by body movement in a majority of species. An interesting variant of blow delivery is noted for *Campephilus principalis* by Allen & Kellogg (1937) and Tanner (1942). This species forages largely by knocking off flakes of bark with sideways blows to reveal insects underneath.

Several species, notably the Acorn woodpecker *Melanerpes formicivorus* and *Dendrocopos* spp. open nuts, acorns and fir cones by wedging them into cracks or holes in bark, then attacking them with the bill. An interesting account of the development of this behaviour in a captive *D. major* is given by Sielmann (1958). Nuts were carried to the chosen 'anvil' in the bill; if the anvil was inadequate, the nut was held under the breast feathers while the bill was used to chisel out more wood. Pine cones were set upright, and the scales broken off one by one, while seeds were picked out with bill or tongue.

Sielmann (1958) describes the use made of the tongue by several European species as revealed by sophisticated cinematography. A feature of particular interest emerging from these observations is the brief duration of most tongue movements. Although these can be forceful enough to impale beetle larvae, or to create a 'drumming' noise on the side of a box housing a captive *Dryocopus martius,* tongue protrusion is not long sustained, but consists instead of a series of very rapidly repeated darting extensions. Sielmann suggests that this is due not to any inability to maintain the tongue in a state of protrusion, but to the necessity for keeping it adequately coated with the sticky secretion from the highly developed salivary glands.

Part 2

Anatomy

Osteology and arthology of the skull

Literature concerning functional aspects of the skull structure among birds in general is discussed more fully in Part 3 (pp. 399–402), but some important papers may be briefly noted here. Barnikol (1952) dealt with overall form of the skull, Bock (1964) with cranial kinesis and Yudin (1961) with movements of the mandibular rami. Kinetic stops were reviewed by Fisher (1955) and secondary articulation of the mandible by Bock (1960*a*). The lacrimal-ectethmoid complex was thoroughly surveyed by Cracraft (1968), who should be referred to for details of the complex and its modifications in the various families of Coraciiformes and Piciformes. Studies on probing adaptations in the Charadrii (Burton 1974*a*) and gaping adaptations in the Icteridae (Beecher 1953*a*) and Callaeidae (Burton 1974*b*) are of special relevance to the Upupidae and Phoeniculidae.

Descriptive and comparative cranial osteology of birds belonging to the Coraciiform-Piciform assemblage has been well covered in the literature, although functional studies are mainly confined to the Picidae. A good summary of nineteenth century literature and views is given by Beddard (1898). Many of the papers from this era dwelt largely on palatal structure, pursuing the ideas first introduced by Huxley (1867). Particular attention was given to the woodpecker palate, with discussions by Garrod (1872), Parker (1875) and Shufeldt (1891). Other important studies include those of Murie (1872*a* & *b*, 1873) on various Coraciiform families, and of Shufeldt (1884) on *Ceryle alcyon.* Publications on various aspects of osteology in the two orders have continued to appear at intervals in the present century, and most of these are mentioned in the reviews of literature included by Sibley and Ahlquist (1972). Important general studies include those by Lowe (1946, 1948) and Verheyen (1955*a* & *b*), while J. Steinbacher (1937) investigated the Galbulidae and Bucconidae, and interest in the Picidae has continued with papers by Burt (1930), Beecher (1953*b*), Spring (1965) and Zusi & Marshall (1970). The study of rollers, ground-rollers and cuckoo-rollers by Cracraft (1971) included a thorough examination of cranial osteology. A detailed and important work on the skull of a single species of hornbill is that by Manger Cats-Kuenen (1961) dealing with *Rhinoplax vigil.*

Ligaments associated with jaw articulations and other regions of the skull have been surveyed by Lebedinsky (1921) and Bock (1964). Those occurring in the Coraciiformes and Piciformes are listed below; they are present throughout, unless otherwise stated, in which case their distribution is given in the family by family summary of skull morphology which follows.

1. The postorbital ligament runs from the tip of the postorbital process to the external process of the mandible, slightly anterior to its articulation with the quadrate. It is absent or reduced in a number of the families studied here.

2. The occipitomandibular ligament is situated at the dorso-medial edge of M. depressor mandibulae, running from the exoccipital process to the posterior face of the internal process of the mandible.

3. The external jugomandibular ligament is a short band connecting the posterolateral face of the jugal bar with the external process of the mandible. It passes superficial to the postorbital and internal jugomandibular ligaments. It is absent in the Picinae, and very weak in the Jynginae and Picumninae.

4. The internal jugomandibular ligament takes the form of a strong band running around the posterior edge of the interface between quadrate and mandible at their articulation. At its lateral end it is attached to the jugal bar, anterior to the external jugomandibular, and medially to the posterodorsal rim of the mandible. Sesamoid bones are commonly found within the ligament (see e.g. Burton 1973).

5. The quadratomandibular ligament is apparently unique to the Bucerotidae (q.v.). It

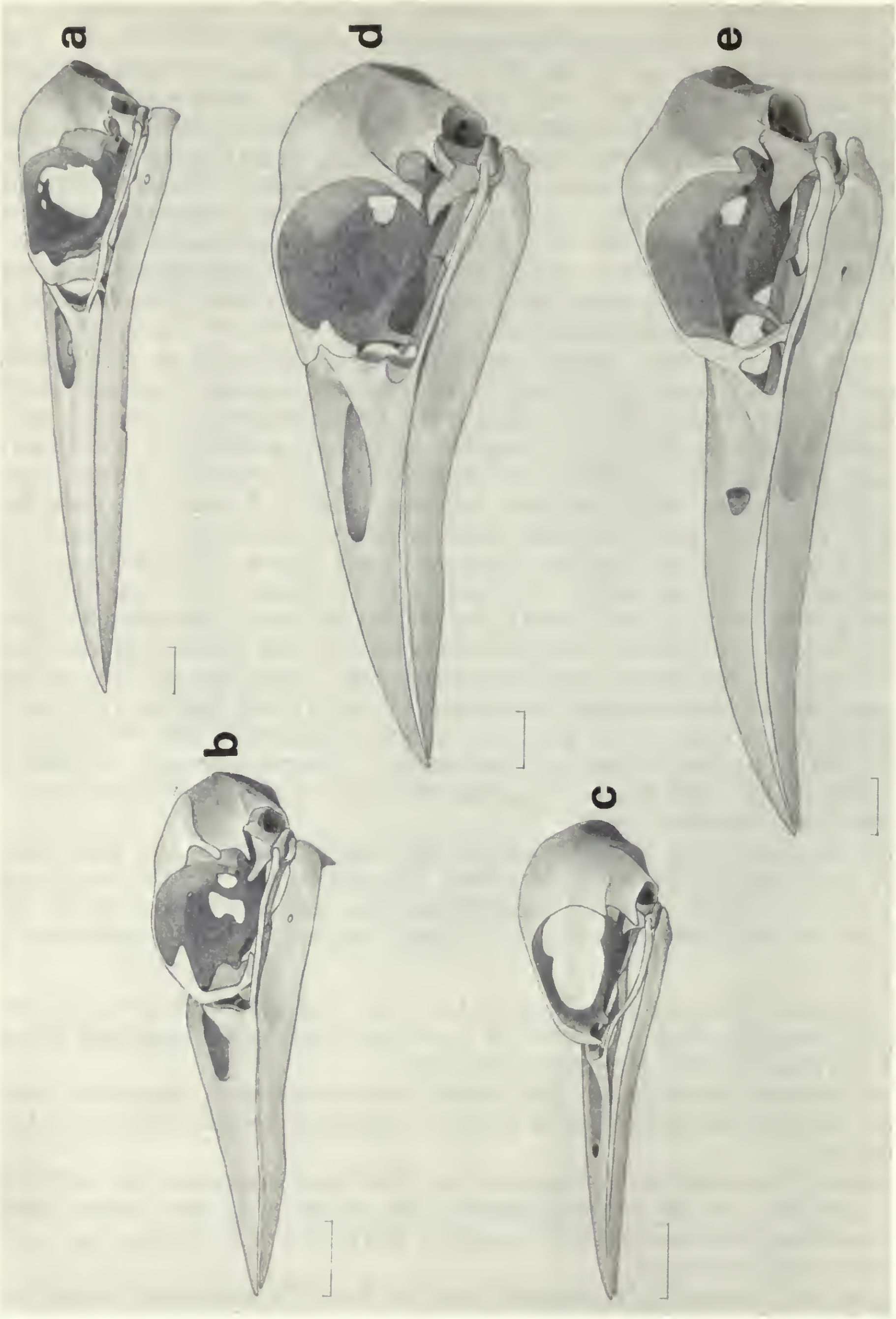

Fig. 1 Skulls in lateral view: a, *Alcedo atthis*; b, *Halcyon concreta*; c, *Todus todus*; d, *Momotus mexicanus*; e, *Nyctiornis amicta*. Scale line = 10 mm. in b., 5 mm. in remainder.

runs from the quadrate body to the medial dorsal surface of the mandible, ventral to M. adductor mandibulae externus. (See Starck, 1940: 610).

6. The lacrimojugal ligament, connecting the ventral tip of the lacrimal with the jugal bar, is scarcely defined as such in families surveyed here, although there is normally some connective tissue linkage between the lacrimal-ectethmoid complex and the jugal bar. The lacrimal itself is absent or vestigial in several families of Coraciiformes and Piciformes (Cracraft, 1968).

7. The subocular ligament, running from the lacrimal to the postorbital process is generally represented by a rather diffuse sheet of connective tissue, though in some cases it is strong enough to possess a distinct point of attachment in the form of a small spur on the anterior edge of the postorbital process.

8. The opisthotic ligament, confined to the Picinae, running from the posterior lateral rim of the auditory capsule to the external process of the mandible.

Snap closing jaw ligaments like those described from some Tyrannidae by Bock & Morony (1972) have not been found, though the quadratomandibular ligament of the Bucerotidae occupies a similar situation.

ALCEDINIDAE. Bill generally long and stout (short and deep in *Clytoceyx*), sharply pointed, and with the tomia recurved anteriorly in many Daceloninae. In *Halcyon torotoro* and *H. megarhyncha,* the tomia are irregularly serrated anteriorly. *Melidora* has the upper jaw hooked at the tip, the hook ending bluntly with a U-shaped cross section as in some Bucconidae. Thoroughly desmognathous, the maxillopalatines fused over a considerable distance in the midline. Skull shows some approach to the 'streckschädel' form described by Barnikol (1952) in various fisheaters, with long pterygoids lying in almost the same plane as palatines, sphenoid rostrum and tomia, and the quadrate rotated backwards, its otic articulation lying well posterior to the orbit. This skull form is particularly marked in the Alcedininae and Cerylinae, and the orbital process of the quadrate is narrowed or vestigial in these subfamilies. Medial condyle of the quadrate oval, not remarkably deep. Retroarticular process barely indicated.

Medial brace (see Bock, 1960*a*) well developed. Postorbital ligament lacking in Alcedininae, feeble or lacking in *Chloroceryle,* fairly stout in Daceloninae.

TODIDAE. Bill long, flattened and rather wide. Not desmognathous, although the maxillopalatines lie close together in the midline. Palatines reduced to frail struts for much of their length. Quadrate with short but broad orbital process, moderately deep, rounded medial condyles. Posterior cranium high, sloping down steeply above the orbits to the fronto-nasal hinge. No retro-articular process.

Medial brace present but feeble. Postorbital ligament narrow but distinct.

MOMOTIDAE. Bill generally robust and somewhat downcurved, with the tomia more or less serrated in their basal two-thirds. The serrations are coarse and tooth like in *Momotus* and *Baryphthengus,* finer (but more numerous) in other genera, especially *Electron.* Unlike many other birds (e.g. toucans) with bill serrations, these projections scarcely slope backwards, but are nearly at right angles to the tomium. In *Electron,* the bill is greatly widened and flattened.

Desmognathous, though midline fusion of the maxillopalatines seems incomplete in some specimens of *Momotus momota.* Quadrate with fairly long but broad orbital process, with an extensive medial edge for attachment of M. pseudotemporalis profundus. Medial condyle oval and deep, extending well ventral to the pterygoid articulation. Postorbital and zygomatic processes strongly developed. Medial brace and postorbital ligament well developed.

MEROPIDAE. The bill is long, moderately decurved and tapering to a sharp point. Fully desmognathous, with a long region of fusion. The posterior cranium extends well posterior to the foramen magnum, and high above the orbit, sloping down very steeply to the fronto-nasal hinge. This profile is less pronounced in *Nyctiornis,* in which the skull is also generally more robustly constructed. Orbital process of the quadrate short and broad, with a long

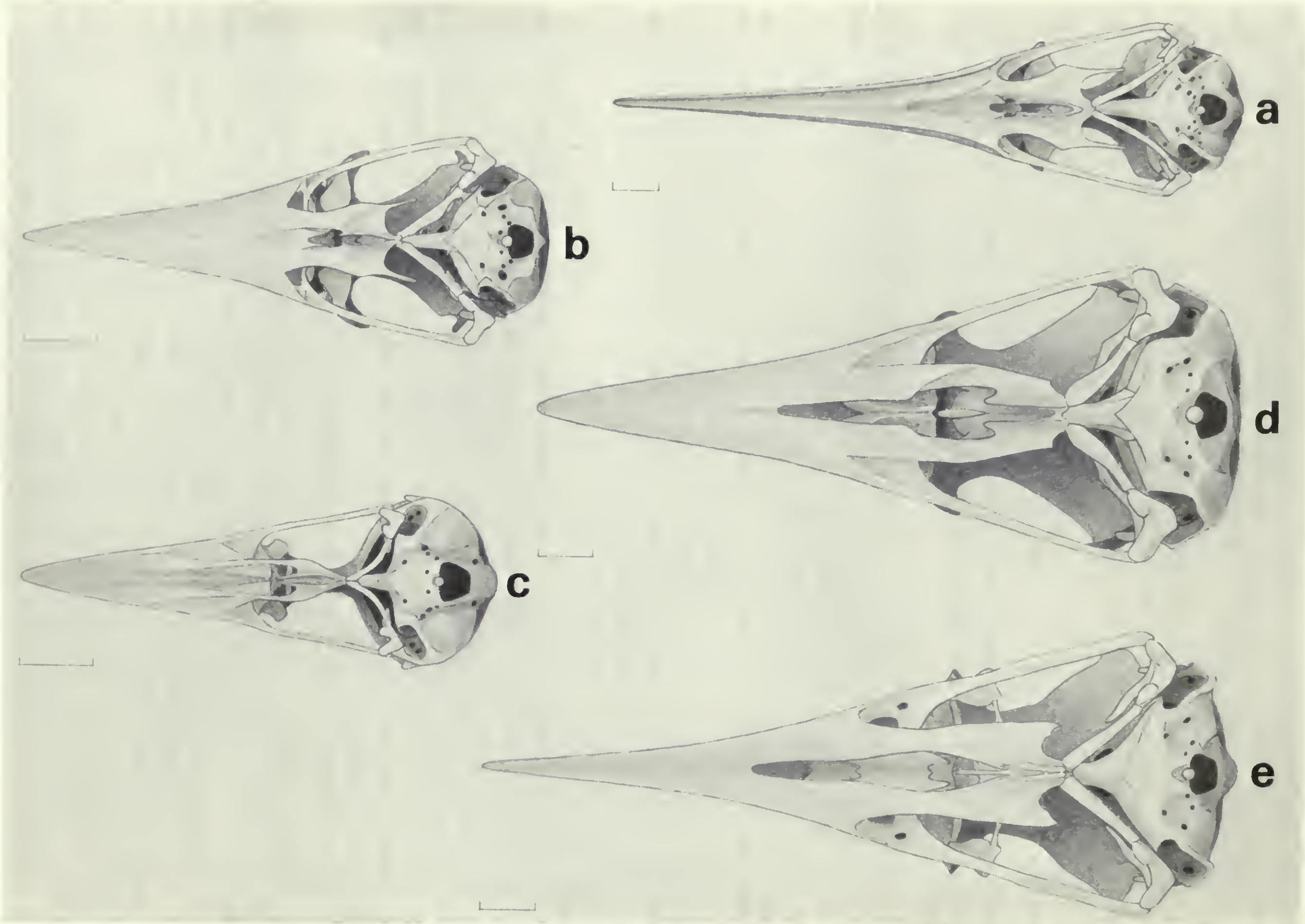

Fig. 2 Skulls in ventral view: a, *Alcedo atthis;* b, *Halcyon concreta;* c, *Momotus mexicanus;* e, *Nyctiornis amicta.* Scale line = 10 mm. in b., 5 mm. in remainder.

medial edge. Medial condyle a narrow oval in section, and deep, extending well ventral to the pterygoid articulation, and somewhat produced anteriorly to give a hook shaped profile when viewed laterally. No retroarticular process. Medial brace present, postorbital ligament rather weak.

LEPTOSOMATIDAE. The Cuckoo-roller's bill is of medium length and fairly deep, resembling those of typical Coraciidae except in the anterior placement of the nostril. Strongly desmognathous, with wide palatines, and the quadrate with a short, fairly broad postorbital process. Medial condyle oval, rather narrow and deep. Orbits relatively very large. The postorbital process is long, reaching the jugal bar, but without an anterior spur for the suborbital process. No retro-articular process. Postorbital ligament stout; medial brace absent. For a comparison of skull morphology in this and the preceding family see Cracraft (1971).

CORACIIDAE. In *Coracias* and the Brachypteraciinae the bill is typically of moderate length, fairly deep, and with gently decurved tomia. In *Eurystomus* it is shorter, but greatly widened. Completely desmognathous. The quadrate has a short, wide orbital process, and a deep, oval medial condyle. The cranium is generally robust and heavily ossified, with a long, stout postorbital process, usually reaching the jugal bar, but with a small protuberance anteriorly for attachment of the suborbital ligament. The whole skull is markedly broadened in *Eurystomus*, and its palatines are conspicuously expanded. No retroarticular process. Medial brace well developed, postorbital ligament broad.

UPUPIDAE. Bill long, slender, pointed and decurved, with a heavily developed rhamphotheca totally occluding the lumen of the bill for most of its length. Weakly desmognathous, with a narrow zone of maxillopalatine fusion. The quadrate has a short but rather narrow orbital process somewhat expanded at its medial tip, and the thin medial condyle barely projects below the pterygoid articulation. Lateral and posterior condyles are fused into a single crescentic structure. The postorbital process is weak, and lies very close to the zygomatic process. Retroarticular process long, extending well behind the quadrate. Vestigial basipterygoid processes sometimes present.

The postorbital ligament is of moderate breadth and the occipito-mandibular ligament is conspicuously well developed. The medial brace is poorly developed, and oriented more nearly parallel to the long axis of the skull than in other groups.

PHOENICULIDAE. Bill varying from medium length, conical and slightly decurved (*P. aterrimus*) through long and moderately decurved (*P. purpureus, P. bollei*) to long, slender and strongly sickle shaped (*Rhinopomastus* spp.); in all cases, the ramphotheca is strongly developed, occluding the lumen as in *Upupa.* Strongly desmognathous in *Phoeniculus,* less so in *Rhinopomastus.* Quadrate orbital process and condyles as in Upupidae, though lateral and posterior condyles are somewhat more distinct. Postorbital and zygomatic processes very close together, the former much reduced. Retroarticular process very long.

Postorbital ligament moderately developed, very strong occipito-mandibular ligament, but medial brace absent.

BUCEROTIDAE. Despite the great variability of the casque in hornbills, the bill itself is rather similar throughout the family moderately long, deep and laterally compressed, with a more or less decurved profile, and tapering to a point. In *Rhinoplax*, the bill is relatively much shorter and more conical than in other hornbills. The skull is robust and heavily ossified, with a doubly desmognathous palate—that is, with maxillopalatines and anterior palatines solidly welded to form a complete bony roof to the proximal part of the upper jaw. The quadrate has a fairly short and rather pointed orbital process. The medial condyle is rounded, but not especially prominent, the lateral crescentic, but clearly distinct from the deeper posterior condyle. Postorbital process well developed. Vestigial basipterygoid processes in some (Starck, 1940). Retroarticular process varying from moderate to barely indicated.

Postorbital ligament extremely broad, occipito-mandibular ligament strongly developed, medial brace absent. In *Bucorvus,* there appears to be some kinetic coupling via the structure

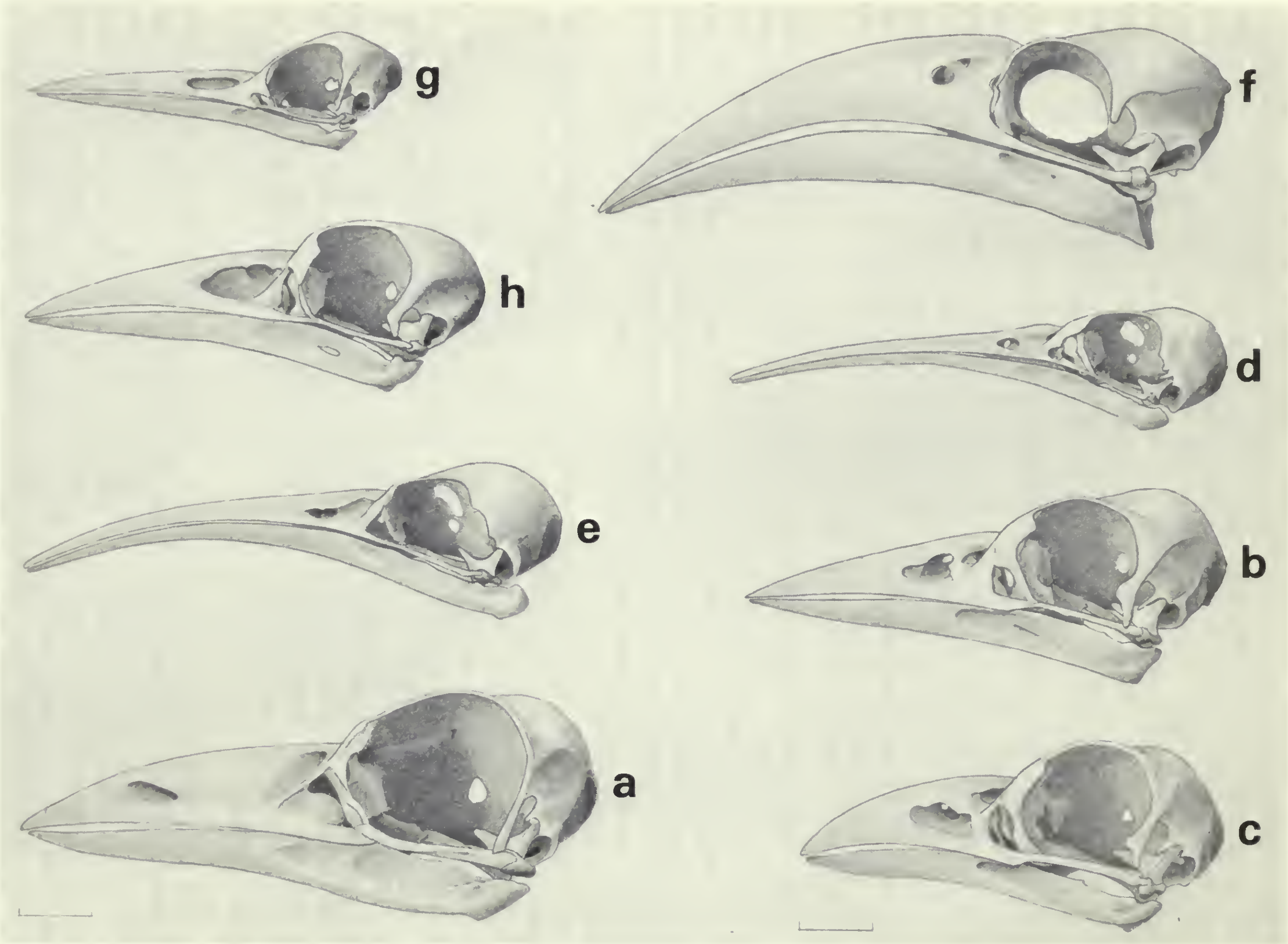

Fig. 3 Skulls in lateral view: a, *Leptosomus discolor;* b, *Coracias benghalensis;* c, *Eurystomus orientalis;* d, *Upupa epops;* e, *Phoeniculus purpureus;* f, *Tockus fasciatus;* g, *Galbula leucogastra;* h, *Monasa atra.* Scale lines = 10 mm: all to same scale.

of the quadrate/mandible articulation; in a dried skull, the lower jaw stays firmly in place once fitted, and in life this would seem to make it impossible for one jaw to move independently of the other. The quadratomandibular ligament appears to be unique to this family, although possibly analogous to one of the snap closing jaw ligaments described by Bock & Morony (1972) in the Tyrannidae.

Galbulidae. Bill typically long, slender, sharply pointed and straight. Much deeper and heavier in *Galbalcyrhynchus,* with a strong dorsal ridge; shorter, deep and somewhat decurved in *Jacamerops.* Fully desmognathous, tending to doubly desmognathous in *Galbalcyrhynchus.* Posterior cranium extends well posterior to the foramen magnum, and dorsal to the orbit, producing a sloping profile as in the Meropidae, though less pronounced. This feature is less obvious in the deep billed *Galbalcyrhynchus,* though the rearward projection of the occipital region is still marked. Quadrate with a short and very broad orbital process which has a long medial edge. Medial condyle narrow and deep, extending well ventral to the articulation with the pterygoid. Postorbital process long and stout, nearly reaching the jugal bar. No retroarticular process. Postorbital ligament fairly strong. Medial brace absent.

Bucconidae. Bill very variable in form; heavy, shrike like and slightly hooked (e.g. *Notharcus*); moderately long and slightly decurved (*Monasa*); long and rather flattened (*Nonnula)*; short, broad and slightly decurved (*Chelidoptera*). In hook billed types, the hook ends bluntly, with a U-shaped cross section, which may be more or less developed into a notched tip; this is especially well shown in *Notharcus.* The lower jaws of hooked billed puffbirds are often emarginated at the tip.

Strongly desmognathous. Quadrate with a very short but broad orbital process, its wide medial edge nearly in line with the posterior edge, giving a rather pointed appearance. The medial condyle is extremely deep, ending in a rounded tubercle, the lateral and posterior condyles merged. The postorbital process is long, curved and broad, often meeting the jugal bar. No retroarticular process. Postorbital ligament strong. Medial brace absent.

Capitonidae. Bills usually massive, of medium length, but wide and deep, with a strongly curved culmen. *Pogoniulus* spp. have bills of more moderate proportions. Notches or serrations on the tomium of the upper jaw are seen in *Lybius* spp., while in *Semnornis* there is a remarkable arrangement in which the hooked tip of the upper jaw fits into the notched tip of the lower when the bill is closed. *Gymnobucco* and *Stactolaema* spp. have a sharp raised ridge on the base of the culmen in the males.

Most barbets have divided palates, though the maxillopalatines have a narrow region of fusion in some *Pogoniulus* spp., *Capito, Eubucco* and *Semnornis.* The vomer has a broad, bifurcated tip resembling that of passerines; hence, the palate may be termed aegithognathous (Beddard, 1898). The quadrate has a long, slender orbital process. The medial condyle does not project far below the pterygoid articulation, but in some species of *Megalaima* it has a sharply defined lateral edge which engages with the lower jaw to give some measure of kinetic coupling. A postorbital ligament is, however, absent in all barbets examined. The postorbital process is long and well defined, and lateral and posterior quadrate condyles are more or less merged into a single S-shaped ridge. The medial brace is absent.

Indicatoridae. The bill is of medium length and fairly robust except in *Prodotiscus*, where it is weak and somewhat decurved. The skull is generally similar to that of the Capitonidae, though more lightly constructed and less heavily ossified than in most barbets. The maxillopalatines remain separate; the quadrate has a slender orbital process, a shallow medial condyle, and its lateral and posterior condyles are merged as in barbets. The junction of pterygoid and palatine has a distinctive form (shared with the Picidae), in which the pterygoid foot is elongated, overlapping the posterior end of the palatine dorsally and medially for a considerable distance. The postorbital ligament is weak, but distinct, and the postorbital process well developed. There is no medial brace.

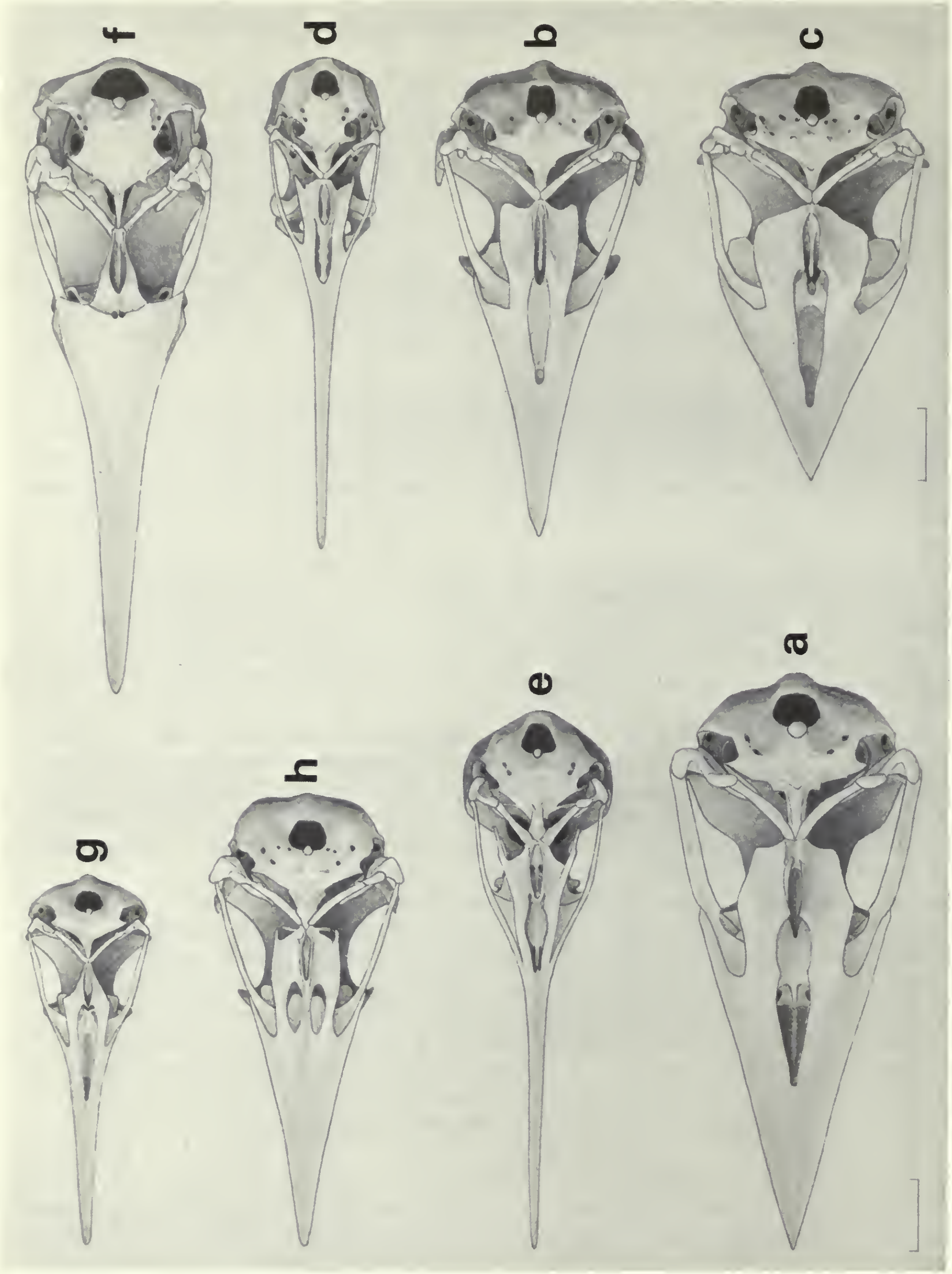

Fig. 4 Skulls in ventral view: a, *Leptosomus discolor*; b, *Coracias benghalensis*; c, *Eurystomus orientalis*; d, *Upupa epops*; e, *Phoeniculus purpureus*; f, *Tockus fasciatus*; g, *Galbula leucogastra*; h, *Monasa atra*. Scale lines = 10 mm: all to same scale.

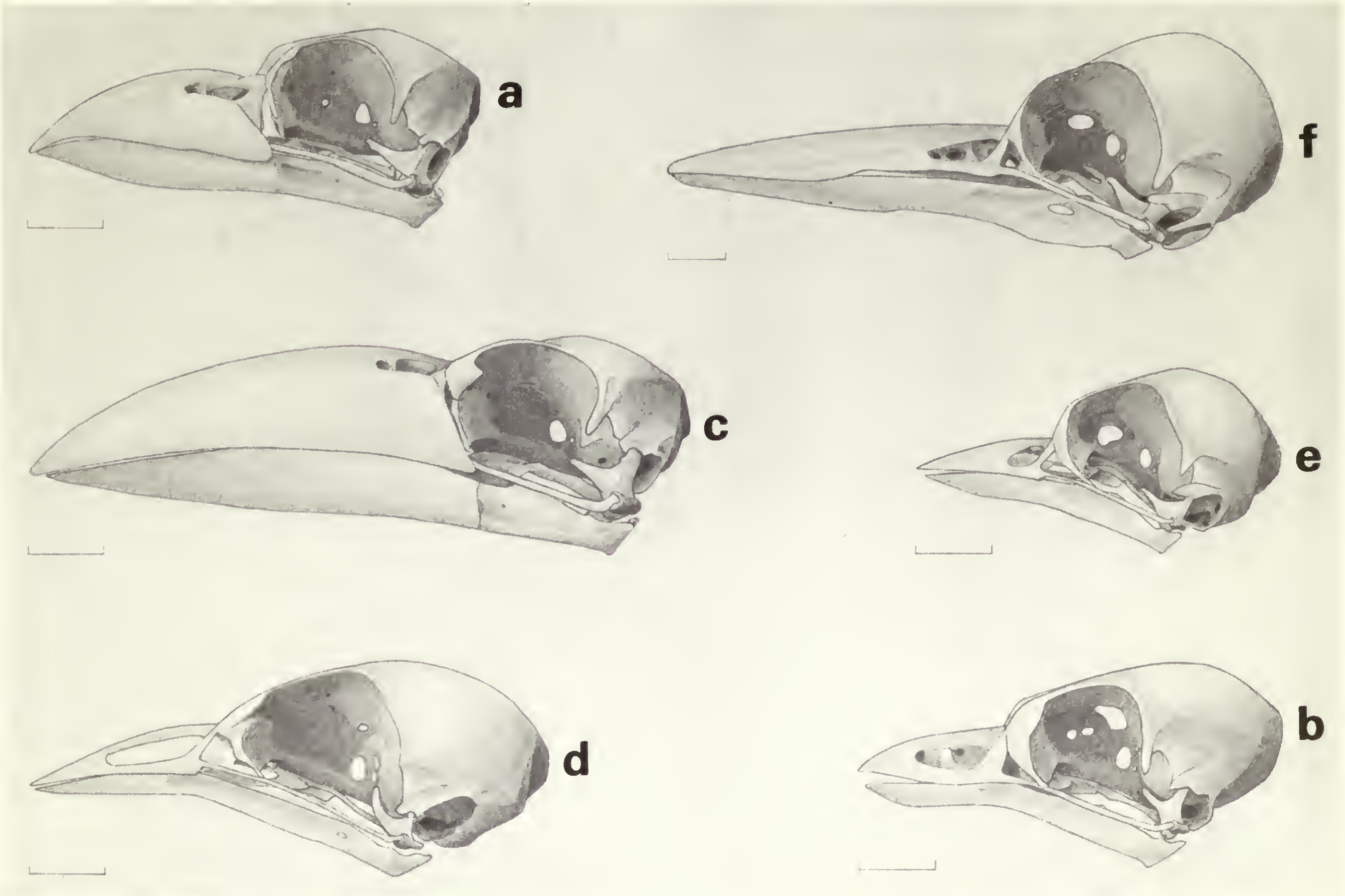

Fig. 5 Skulls in lateral view: a, *Psilopogon pyrolophus;* b, *Indicator minor;* c, *Selenidera langsdorffi;* d, *Jynx torquilla;* e, *Sasia abnormis;* f, *Dendrocopos major.* Scale lines = 10 mm. in a. and c., 5 mm. in remainder.

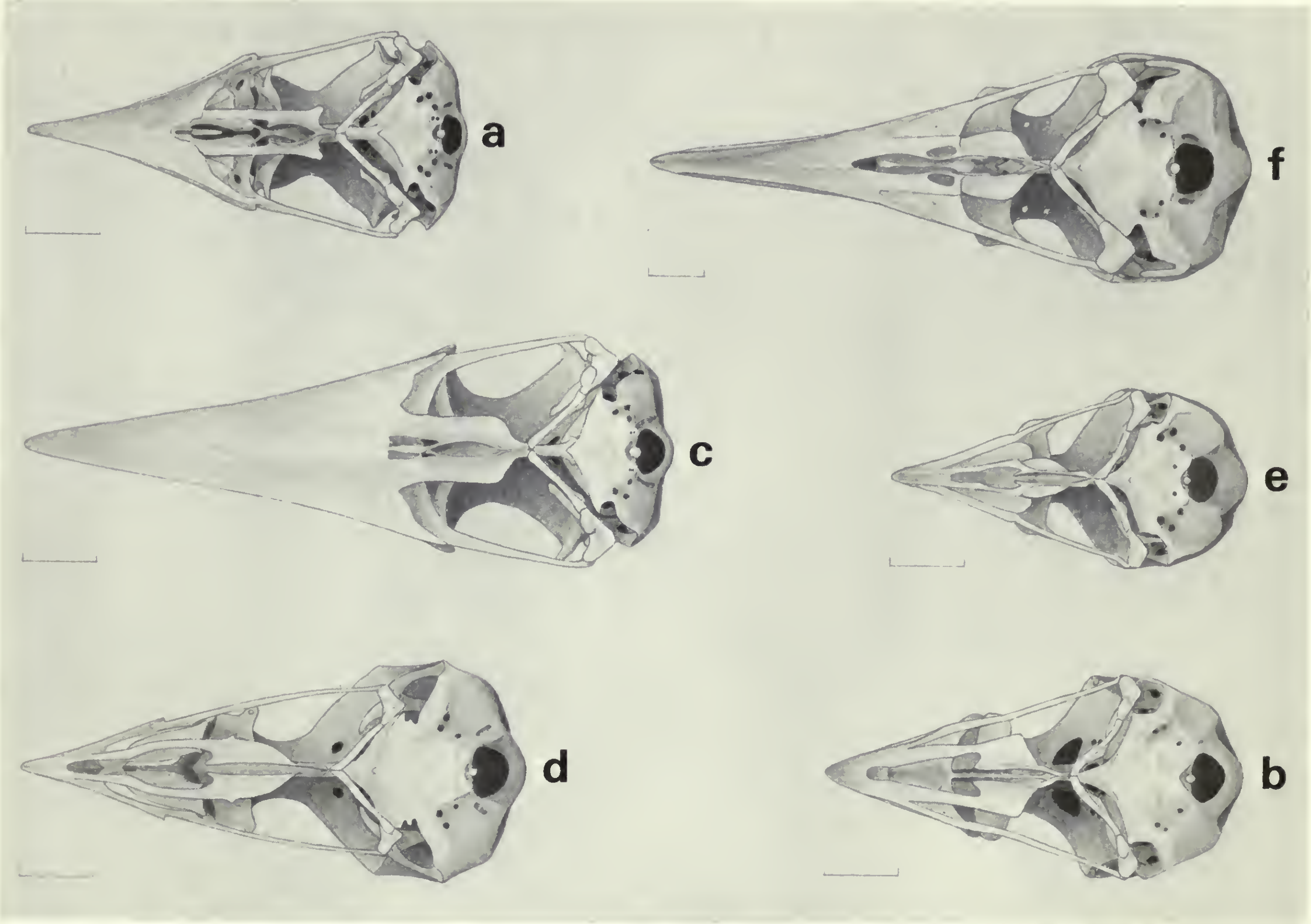

Fig. 6 Skulls in ventral view: a, *Psilopogon pyrolophus;* b, *Indicator minor;* c, *Selenidera langsdorffi;* d, *Jynx torquilla;* e, *Sasis abnormis;* f, *Dendrocopos major.* Scale lines = 10 mm. in a. and c., 5 mm. in remainder.

RAMPHASTIDAE. The use of *R. toco* as an advertising symbol has made the bills of toucans familiar even to non-ornithologists. All are basically similar—long and deep, with a strongly decurved tip. There is less lateral compression than in the superficially somewhat similar bills of the Bucerotidae. The upper tomium is strongly serrated, the lower more weakly; the serrations slope more steeply anteriorly than posteriorly. In *Andigena laminirostris* the tip of the lower mandible ends with a U-shaped cross section which slightly overlaps the curved tip of the upper on each side.

The palate is thoroughly desmognathous, with the maxillopalatines fused along a considerable length of the midline, and the anterior part of the palatines and vomer fused onto the continuous bony sheet lining the upper jaw. As in the Capitonidae the orbital process of the quadrate is long and slender; the medial condyle fairly shallow, and the posterior and lateral condyles merged into a single curved ridge. As in the barbets too, the postorbital ligament is absent, although there is a strong postorbital process. The medial brace is also absent.

PICIDAE. Extensive differences exist between *Jynx* and the remainder of the family. The bills of typical woodpeckers and piculets are short to moderately long, straight, and tapering evenly to a blunt point; the rhamphotheca is hard and well developed. The bills of wrynecks resemble those of woodpeckers in their straight, pointed form, but are proportionately much smaller and more lightly constructed, with large bony nares, and a minimum of rhamphothecal reinforcement.

Other features of skull structure also show considerable disparity between *Jynx* on the one hand and the woodpeckers and piculets on the other. Their principal common features are in palatal structure; all have reduced maxillopalatines and reduced or absent vomer. (For discussion of the latter see Beddard, 1898: 186–187). As in the Indicatoridae the pterygoid foot overlaps the palatine extensively at its posterior end. However, the following specialized features are limited to the Picinae and Picumninae: a pronounced, or even overlapping, forehead at the fronto-nasal hinge; a spur on the pterygoid from which arises part of M. protractor; a quadrato-jugal articulation which is extended posteriorly behind the lateral condyle, with consequent enlargement of the quadrate body, especially in the Picinae; and, in the Picinae only, a strong forwardly directed process extending from the posterior lateral rim of the auditory capsule, with ligamentous attachment to the external process of the mandible. In some species this process apparently articulates with the posterior surface of the lateral process of the quadrate, which is markedly broadened in woodpeckers.

The orbital process of the quadrate is long and slender in all three sub-families, but is strongly curved in the Jynginae. The postorbital process and ligament are weak, though distinct, in *Jynx*, but both are quite strongly developed in woodpeckers and piculets. The medial brace is absent in all.

Jaw muscles

The basis for most detailed studies of avian jaw muscles was laid down by Lakjer (1926). His system of nomenclature is adhered to as far as possible, but with modifications stemming from more recent work, notably that of Starck & Barnikol (1954) and Richards & Bock (1973). As noted in the introduction, N.A.A. terms (Baumel *et al.*, 1979) are given in headings where they differ from terms used here. The descriptions given here are effectively the first for most families of Coraciiformes and Piciformes with the exception of those for the Bucerotidae (Starck, 1940) and Picidae (Beecher, 1953*b*).

M. adductor mandibulae externus (abb: M.add.mand.ext.)

This muscle is of complex structure, and several subdivisions can be recognized. Various systems of terminology and criteria have been employed by different authors for naming and distinguishing these subdivisions. The system followed here is that used by Richards & Bock

(1973). Starck & Barnikol (1954) demonstrated the presence of three major aponeuroses in the muscle in birds of several orders. These aponeuroses are recognizable in the families considered here, and the numbering used corresponds to that of Stark & Barnikol. (See also Table 1).

M. adductor mandibulae externus rostralis (M.a.m.e.rost.) is the most dorsal portion of the muscle. It can be further divided into three parts:

(a) *M. adductor mandibulae externus rostralis temporalis* (M.a.m.e.rost.temp.) has a fleshy origin from the temporal fossa, from the base of the postorbital process, and from the dorsal surface of Aponeurosis 2. It inserts on the coronoid process of the mandible via a flattened tendon (Aponeurosis 1) which begins within the temporal region as the raphe of a bipinnate fibre arrangement.

(b) *M. adductor mandibulae externus rostralis lateralis* (M.a.m.e.rost.lat.). Origin is from the lateral edge of the zygomatic process and the dorso-lateral surface of Aponeurosis 2. Insertion is made either through the lateral part of Aponeurosis 1, or through an aponeurosis covering the antero-lateral surface of the muscle, and continuous medially with Aponeurosis 1.

Table 1. Divisions of M. adductor mandibulae externus used in the present paper, and their equivalents in some previous studies. Further tables of synonymy are given by Starck and Barnikol (1954). See also Baumel *et al.*, 1979.

	Burton, 1974 (Charadrii)	Starck & Barnikol 1954 (several orders)	Lakjer (1926); Goodman & Fisher, 1962 (Anatidae)
M.a.m.e. rostralis	Part M + Part A dorsal	Aponeurosis 1 portion	Part of superficialis
M.a.m.e. rostralis temporalis	Part M, external temporal	Aponeurosis 1 portion, external temporal	superficialis, 1a portion (Levatoranguli oris).
M.a.m.e. rostralis lateralis	Part A, dorsal	Aponeurosis 1 portion	not present
M.a.m.e. rostralis medialis	Part M, rostral	Aponeurosis 1 portion	medialis
M.a.m.e. postorbital lobe, dorsal part	Not named; absent in most species	Aponeurosis 1 portion	superficialis, 1c portion (retractor anguli oris)
M.a.m.e postorbital lobe, ventral part.	Not named; absent in most species.	Aponeurosis 1 portion	superficialis, 1b portion
M.a.m.e. ventralis	Part A, ventral	Aponeurosis 2 portion	Included with superficialis 1a portion; rost. temp. + vent. treated as a bipinnate muscle.
M.a.m.e. caudalis	Part B	Aponeurosis 3 portion	M. adductor mandibulae posterior
M.a.m.e. caudilis, lateral expansion	Part B, lateral expansion	Aponeurosis 3 portion	profundus

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*In discussions throughout this paper I shall use these terms in their German form, to indicate their origin clearly, to avoid possible ambiguities inherent in their English translations, and because they are less clumsy.

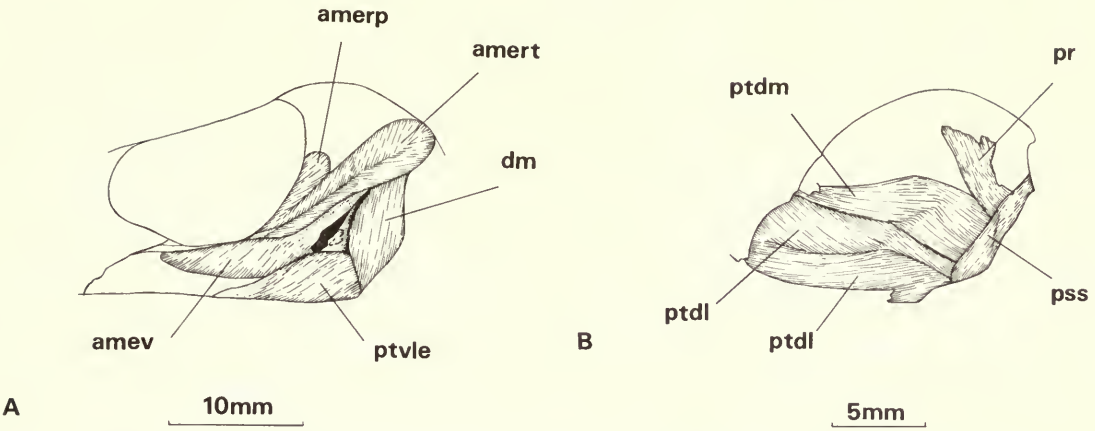

Fig. 7 *Chloroceryle americana,* jaw musculature: A, lateral view; B, dorsal view.

(*c*) *M. adductor mandibulae externus rostralis medialis* (M.a.m.e.rost.med.) originates from the lateral edge of the posterior will of the orbit and the medial edge of the temporal fossa. The origin is fleshy, and may also involve an aponeurosis on the medial surface. The insertion is on the anterior coronoid process, posterior and medial to that of M. adductor mandibulae externus rostralis temporalis, usually via a lateral aponeurosis which is continuous with Aponeurosis 1.

M. adductor mandibulae externus ventralis. (M.a.m.e.vent.) Origin is from the medial and ventral surfaces of Aponeurosis 2, which begins as a strong flat tendon arising from the zygomatic process, and fans out anteriorly over the lateral surface of the muscle. The main region of insertion is a wide area on the lateral side of the mandible; fibres arising more posteriorly run forwards and downwards to insert on the dorsal surface of Aponeurosis 3 and could equally be considered with M.a.m.e. caudalis.

M. adductor mandibulae externus caudalis. (M.a.m.e.caud.) Origin is fleshy from the otic process of the quadrate, and insertion is usually made principally via Aponeurosis 3 which lies on the dorso-lateral side of the muscle. The insertion is on the dorsal edge of the mandible, behind and below that of Aponeurosis 1. In some species, there is an additional aponeurosis of insertion (Aponeurosis 3a) on the medio-ventral surface of the muscle; it may be separate from Aponeurosis 3 at the insertion, or may fuse with it. There is frequently an additional aponeurosis (Aponeurosis 4) in the muscle, which arises on the otic process, and functions as the raphe of a bipinnate fibre arrangement. In the Picidae, this aponeurosis, and the part of the muscle medial and ventral to it, are expanded anteriorly to insert widely on the lateral surface of the mandible. This will be further explained under the family heading.

CORACIIFORMES

The main general points of difference from the Piciformes concern the lateral region of the muscle. M.a.m.e.rost.lat. is never extensively developed, and in many cases, scarcely to be distinguished. M.a.m.e.vent. fans out further anterior, so that it does not usually conceal M.a.m.e.caud., as in many Piciformes. M.a.m.e.caud. itself is narrow, but usually bipinnate. Aponeurosis 3 may join Aponeurosis 1 medially, and the dorsal edge of Aponeurosis 4 commonly joins Aponeurosis 2 at its medial edge.

ALCEDINIDAE. *Alcedo atthis.* M.a.m.e.rost.temp. is highly developed, the right and left muscles meeting in the midline, at the back of the skull; Aponeurosis 1 extends far back in the temporal region as the raphe of a strongly marked bipinnate system. There is a well developed distinct slip (referred to here as the postorbital lobe) also bipinnate, arising at the

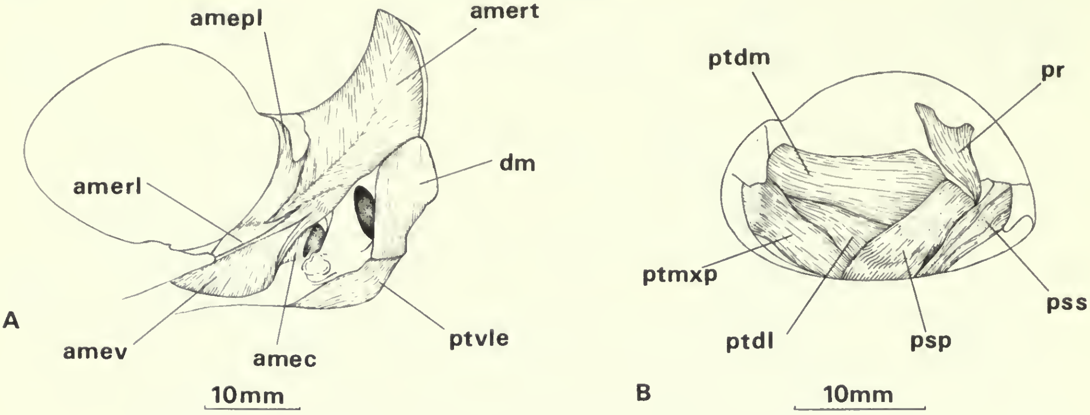

Fig. 8 *Dacelo gaudichaud*, jaw musculature: A, lateral view; B, dorsal view.

lateral edge of the posterior orbital wall, its raphe arising from a blunt process corresponding in position with the postorbital process, the postorbital ligament being absent. The dorsomedial surface of the postorbital lobe is covered by an aponeurosis which joins Aponeurosis 1 anteriorly. M.a.m.e.rost.lat. is absent. M.a.m.e.caud. is small and has only one aponeurosis (Aponeurosis 3), which is vertically oriented. It inserts through this and a small fleshy attachment.

Other members of the family show an essentially similar structure, including a slip arising from the postorbital process, although a postorbital ligament is present in the Cerylinae and Daceloninae. In these families also, a distinct, though small M.a.m.e.rost.lat. can be distinguished, fused posteriorly with M.a.m.e.rost.temp. It is best developed in *Dacelo*, in which it is aponeurotic on its lateral surface, and extends a little way over the dorsal part of M.a.m.e.vent. In the Daceloninae, M.a.m.e.caud. is better developed; Aponeurosis 4 is present and an Aponeurosis 3a was discernible in *Halcyon chloris.*

TODIDAE. *Todus viridis.* The origin of M.a.m.e.rost.temp. is much reduced in extent, but retains clear bipinnate structure. M.a.m.e.rost.lat. is more substantial than in most families of the order, and its aponeurosis of insertion is, in effect, the lateral part of Aponeurosis 1 which has no lateral expansion. Aponeurosis 2 is weakly developed. M.a.m.e.caud. is thin and of simple structure, with only one aponeurosis (Aponeurosis 3). Ventrally and medially there is some fusion with M. adductor posterior.

MOMOTIDAE. *Momotus momota.* M.a.m.e.rost.temp. extends back over about half the cranium posterior to the orbit, but is unusually bulky in the orbital region, bipinnate structure continuing well forward into this area; there is also a small but distinct postorbital lobe. M.a.m.e.rost.lat. is also substantial, and has a strong lateral aponeurosis of insertion. M.a.m.e.caud. is much reduced, and only Aponeurosis 3 can be discerned; this is broad and vertically oriented, its medial edge joining Aponeurosis 1 dorsally. There are no fibres medial to Aponeurosis 3. *Electron platyrhynchum* and *Baryphthengus ruficapillus* are similar, but lack a distinct postorbital lobe.

MEROPIDAE. *Nyctiornis amicta.* M.a.m.e.rost.temp. has a long but narrow area of attachment, extending almost to the midline of the cranium posteriorly. It is strongly bipinnate in structure. Aponeurosis 1 is sharply downturned where it reaches the orbit. M.a.m.e.rost.lat. is vestigial, and M.a.m.e.vent. is thus almost completely exposed laterally. M.a.m.e.caud. is bulky and bipinnate, with three aponeuroses; 3 and 3a which insert separately, though close together, and Aponeurosis 4 arises from the origin, its dorsal edge joining the medial edge of Aponeurosis 2.

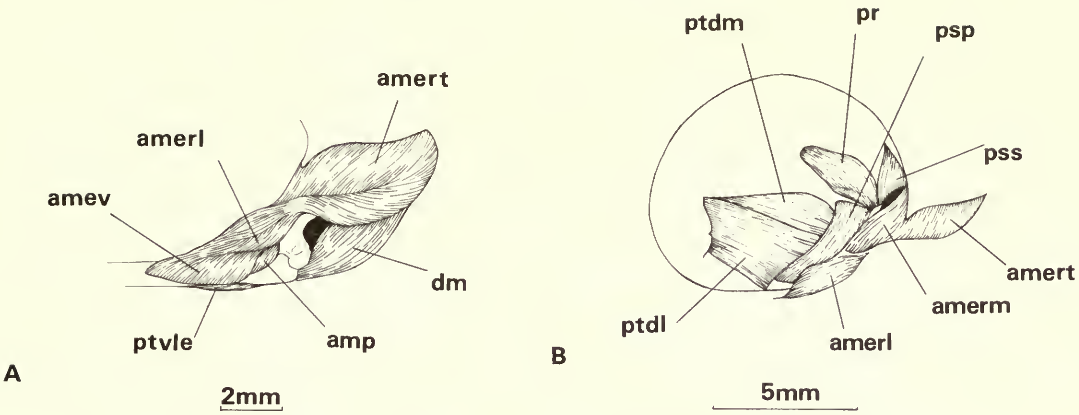

Fig. 9 *Todus todus,* jaw musculature: A, lateral view: B, dorsal view.

Other bee-eaters appear essentially similar. M.a.m.e.rost.temp. is even narrower in other genera, and the downward bend in Aponeurosis 1 at the border of the orbit is absent or unnoticeable. The insertion of M.a.m.e.ext.vent. is generally rather small in extent.

Leptosomatidae. M.a.m.e.rost.temp. has a very limited temporal origin, in which no obvious bipinnate structure can be distinguished. Aponeurosis 1 is partially overlapped in the orbit by fibres of M.a.m.e.rost.med. M.a.m.e.rost.lat. is absent. M.a.m.e.vent. possesses the unusual feature of a small aponeurosis on the lateral side arising from the postorbital ligament (which is extremely broad). This joins Aponeurosis 2 anteriorly; it is largely concealed by a lobe overlapping it laterally from below. This lobe consists of fibres inserting on the dorsal surface of Aponeurosis 3, some arising from Aponeurosis 2, and some on the otic process, and hence part of M.a.m.e.caud. The more medial fibres of M.a.m.e.caud. insert along the medial edge of Aponeurosis 3, which is its only aponeurosis in this family.

Coraciidae. *Coracias benghalensis.* M.a.m.e.rost.temp. covers about three-fifths of the distance between the orbit and the posterior midline of the skull. Its bipinnate structure is not well marked. M.a.m.e.rost.lat. is absent. M.a.m.e.vent. has a rather small area of insertion, covering only about half the depth of the mandible. M.a.m.e.caud. has a double aponeurosis of insertion (Aponeuroses 3 laterally and 3a medially), the two fusing at the point of attachment. Its fibres are arranged bipinnately about Aponeurosis 4.

In *Eurystomus* M.a.m.e.rost.temp. is more extensive, nearly reaching the skull midline; nevertheless, bipinnate structure is not well marked. The insertion of M.a.m.e.vent. is rather larger, and there is a distinct M.a.m.e.rost.lat.; its fibres are short, arising along the dorsal edge of Aponeurosis 2, and running forwards and up at a steep angle to Aponeurosis 1. *Brachypteracias* is similar to *Coracias.*

Upupidae. *Upupa epops.* M.a.m.e.rost.temp. consists of two portions. The main portion, occupying the temporal fossa, is much reduced by comparison with the majority of families included in this study, the temporal fossa itself being extremely small. An additional portion, corresponding to the postorbital lobe described in the Alcedinidae, arises from the base of the postorbital process, and a concave region on the rim of the orbit just dorsal to this. Both the main portion and the dorsal slip are bipinnate. The strong raphe of the dorsal slip arises from the tip of the postorbital process, anterior to the postorbital ligament, while the raphe of the main portion is, of course, Aponeurosis 1. M.a.m.e.rost.med. is narrow and M.a.m.e.rost.lat. is only moderately developed. M.a.m.e.vent. has the normal wide insertion on the mandible. M.a.m.e.caud. is bipinnate, and has lateral and medial aponeuroses of insertion (Aponeuroses 3 and 3a).

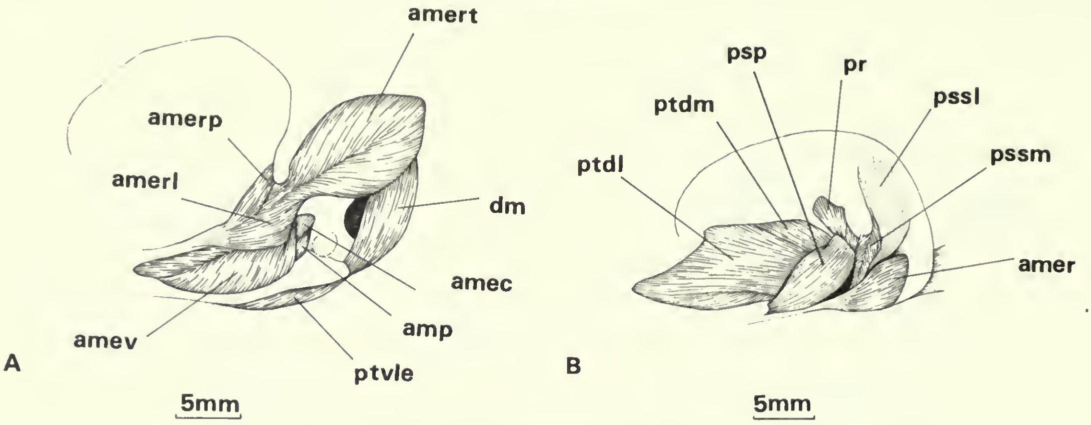

Fig. 10 *Momotus momota,* jaw musculature: A, lateral view; B, dorsal view.

Phoeniculidae. *Phoeniculus purpureus.* As in *Upupa,* the postorbital process is relatively close to the zygomatic process, so that the short temporal portion of M.a.m.e.rost.temp. is very narrow. However, the postorbital lobe is bulkier and more complex in structure, consisting of two parts. The more dorsal of these consists of fibres originating dorsal and anterior to the postorbital process, and these insert via an aponeurosis (1a) situated on the dorsal and medial surfaces, on the dorsal edge of the mandible. The more ventral part consists of fibres originating from the ventral surface of an aponeurosis (1b) attached near the base of the postorbital process. This part fans out across the dorsal lateral surface of the mandible, and aponeurosis 1b covers part of this broad fleshy insertion laterally. Aponeurosis 1 itself is broad, and is extended laterally to provide insertion also for the poorly developed M.a.m.e.rost.lat. M.a.m.e.vent. is much reduced by comparison with most birds. Aponeurosis 2 is weak, and the fleshy insertion on the mandible is a narrow one, between the broad fleshy insertion of the postorbital lobe (ventral portion), and the anterior part of M.a.m.e.caud. This latter division of the muscle inserts by two strong aponeuroses (1 and 3a), the dorsal and lateral one (3) attaching just onto the lateral surface of the mandible. Between them lies a raphe (Aponeurosis 4) which spreads out onto the lateral ventral surface of the mandible, the fibres medial to it making a broad fleshy insertion.

P. aterrimus is generally similar to *P. purpureus,* but the following differences may be noted: The dorsal part of the postorbital lobe does not insert only by Aponeurosis 1a, but has in addition a narrow band of fibres extending and inserting along the dorsal lateral edge of the mandible. Aponeuroses 1 and 3 fuse at the insertion; M.a.m.e.vent. is still more reduced. The lateral lobe covered by Aponeurosis 4 is very large, but Aponeurosis 3a is rather weak.

Rhinopomastus resembles *P. purpureus,* but M.a.m.e.vent. is even more reduced, and the temporal origin is almost absent.

Bucerotidae. *Tockus erythrorhynchus.* M.a.m.e.rost.temp. extends back about two thirds of the distance from the orbit to the midline of the cranium. The insertion of M.a.m.ext. on the mandible is narrow, and limited to its dorsal edge. Aponeuroses 1 and 3 are very strong and prominent, and the insertions of both are clearly visible in lateral view. There is no distinct M.a.m.e.rost.lat. A band of fibres arising at the tip of the postorbital process travels a short way to insert at a large angle on the lateral edge of Aponeurosis 1. M.a.m.e.vent. is much reduced, amounting to only a narrow band of fibres inserting between Aponeuroses 1 and 3; Aponeurosis 2 is moderately developed. M.a.m.e.caud. is strongly bipinnate, and the dorsal edge of its raphe (Aponeurosis 4) joins Aponeurosis 2 medially. There is a strong Aponeurosis 3a inserting medial to Aponeurosis 3, and an additional aponeurosis on the medial surface of M.a.m.e.caud.

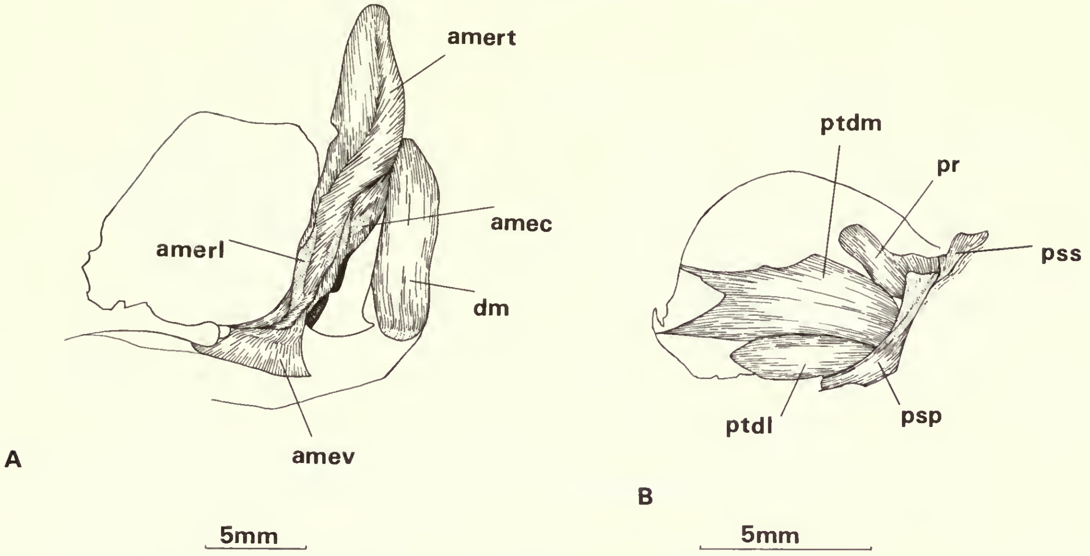

Fig. 11 *Merops superciliosus,* jaw musculature: A, lateral view; B, dorsal view.

PICIFORMES

A feature of the muscle in many Piciformes is the extensive M.a.m.e.lat., which forms a flattened sheet covering much of M.a.m.e.vent., though usually easily separable from it. The anterior part is usually strongly aponeurotic on its lateral surface. M.a.m.e.vent. fans out relatively close to the origin; it frequently conceals the lateral surface of M.a.m.e.caud. Aponeurosis 3 is usually broad, and M.a.m.e.caud. well developed. A raphe (Aponeurosis 4) is often present, but a medial aponeurosis of insertion (Aponeurosis 3a) is lacking in most groups.

Galbulidae. *Galbula dea.* M.a.m.e.rost.temp. has a fairly long area of origin covering about three fifths of the space between the orbit and the posterior midline of the skull. Its structure is clearly bipinnate. M.a.m.e.rost.lat. is absent. Aponeurosis 2 is broad, and the fleshy insertion of M.a.m.e.vent. is extensive, but fans out some distance from the origin. M.a.m.e.caud. is bipinnate; its medial fibres insert on a weak Aponeurosis 3a, which dorsally joins the medial edge of Aponeurosis 1 near the insertion. Aponeurosis 3 itself is narrow. Aponeurosis 4 is fairly well developed, joining Aponeurosis 2 dorsally.

These features—which differ in several respects from the general characters of the Piciformes noted above—are shown with little variation by the various other jacamars examined. In *Jacamerops* and *Galbalcyrhynchus* M.a.m.e.temp. is more extensive, reaching close to the posterior midline of the skull, and Aponeurosis 2 is extensive; In *Brachygalba,* M.a.m.e.temp. is somewhat reduced, covering only about half the posterior cranium.

Bucconidae. *Chelidoptera tenebrosa.* Generally similar to the Galbulidae in most respects. M.a.m.e.rost.temp. extends back about two-thirds of the distance from the orbit to the skull midline. M.a.m.e.vent. is noticeably bulky, but Aponeurosis 2 is not extensive.

Other puffbirds also resemble the Galbulidae (and differ from other Piciformes) in general features. M.a.m.e.rost.temp. reaches the skull midline in *Nystalus* spp. and *Notharcus macrorhynchos,* and nearly as far in *Hypnelos* and *Notharcus tectus.* It is rather short (comparable with *Chelidoptera*) in *Nonnula.* M.a.m.e.vent. is notably bulky also in *Nystalus* and *Notharcus,* and distinctly elongated in *Monasa* spp. M.a.m.e.rost.med. is unusually broad in *Nystalus* spp.

Capitonidae. *Megalaima haemacephala.* M.a.m.e.rost.temp. has an origin extending nearly

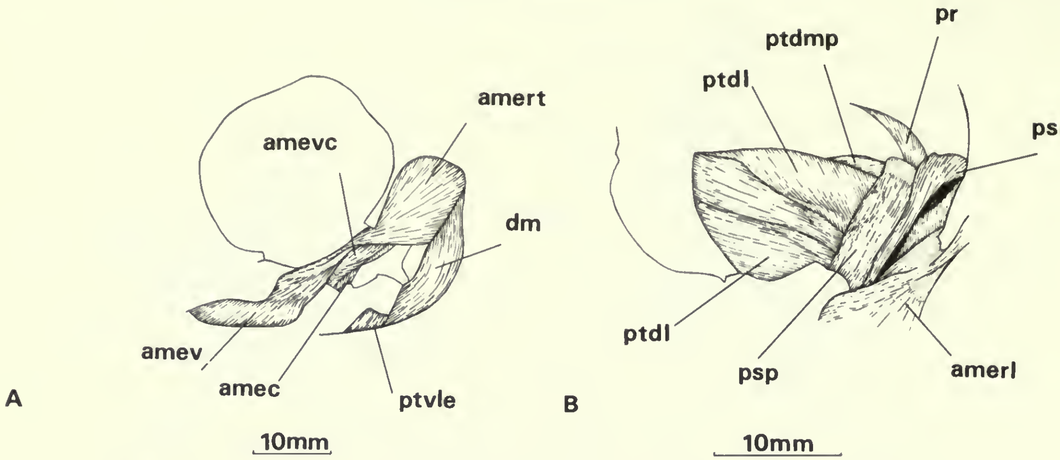

Fig. 12 *Leptosomus discolor,* jaw musculature: A, lateral view; B, dorsal view.

back to the midline, and is clearly bipinnate. M.a.m.e.rost.lat. is wide and flattened, covering more than half the area of M.a.m.e.vent. as seen laterally. Its surface is largely covered anteriorly by a strong aponeurosis continuous dorsally with Aponeurosis 1. M.a.m.e.vent. fans out close to its origin, concealing M.a.m.e.caud. from view laterally. Aponeurosis 3 is broad and vertically oriented, M.a.m.e.caud. forming a rather thin sheet. There is a raphe (Aponeurosis 4), its dorsal edge joining the medial edge of Aponeurosis 2.

The muscle is similar in other barbets examined including *Pogoniulus.* In *Semnornis,* a fleshy slip from M.a.m.e.caud., arising lateral to Aponeurosis 4 extends a short way onto the lateral surface of the mandible.

INDICATORIDAE. *Indicator indicator.* M.a.m.e.rost.temp. extends only about half way to the skull midline. M.a.m.e.rost.med. is bulky, and M.a.m.e.rost.lat. is wide and flattened with an extensive lateral aponeurosis as in barbets. M.a.m.e.vent. has an elongated area of insertion. M.a.m.e.caud. is visible laterally; Aponeurosis 3 is short, and there is a weak bipinnate arrangement, although a clear Aponeurosis 4 cannot be detected. *I. maculatus, I. minor* and *Melichneutes* are similar.

RAMPHASTIDAE. *Selenidera maculirostris.* M.a.m.e.rost.temp. spans about three-quarters of the space between the posterior rim of the orbit and the posterior midline of the skull. Aponeurosis 1 is sharply angled down at the edge of the orbit. M.a.m.e.rost.lat. forms a broad flattened sheet as in barbets, but with a more extensive lateral aponeurosis; this covers much of the lateral surface of M.a.m.e.vent. M.a.m.e.caud is similarly flattened, with a broad, vertically oriented Aponeurosis 3; it is bipinnate, with a distinct Aponeurosis 4, but no Aponeurosis 3a.

Other toucans examined are closely similar.

PICIDAE. *Jynx torquilla.* M.a.m.e.rost.temp. has only a very small area of origin. In the orbital region, Aponeurosis 1 is almost buried by dorsal fibres. M.a.m.e.rost.lat. and M.a.m.e.vent. are similar in their extent and form to those of the Capitonidae and Indicatoridae. M.a.m.e.-caud. is fairly bulky, visible laterally, and weakly bipinnate, though no Aponeurosis 4 can be detected. Aponeurosis 3 is short and superficial, and there is no Aponeurosis 3a.

Dendrocopos major. The origin of M.a.m.e.rost.temp. is small, and there is a vestigial postorbital slip. Aponeurosis 1 is broad dorsally, but partly covered by dorsal fibres; their superficial aponeurosis fuses with Ap.1 anteriorly. M.a.m.e.rost.lat. is fairly narrow. M.a.m.e.vent., also narrow, extends well forward, concealing Aponeurosis 3 which inserts on a prominent ridge on the dorsal lateral surface of the mandible.

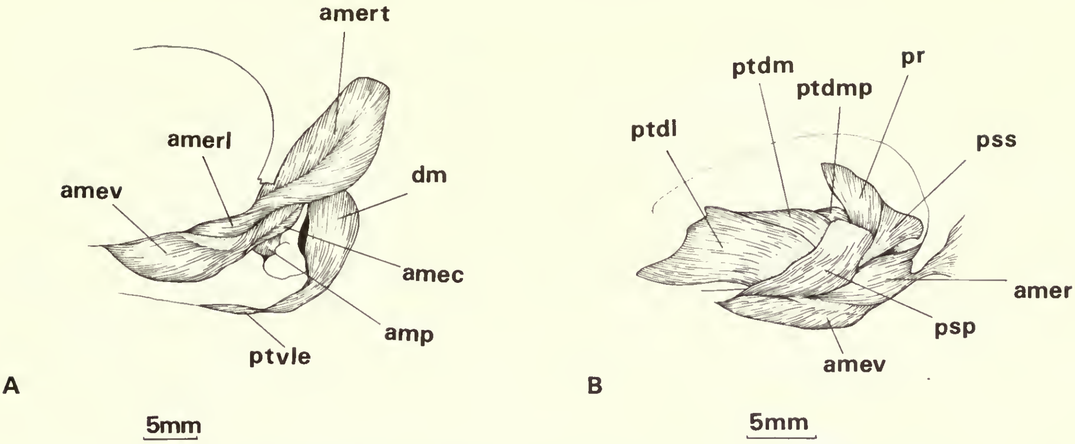

Fig. 13 *Coracias abyssinica,* jaw musculature: A, lateral view; B, dorsal view.

M.a.m.e.caud. is highly developed, and Aponeurosis 4 extends a long way lateral and anterior to the rest of the muscle, with fibres fanning out from its medial surface to insert on the mandible over a wide area ventral and posterior to M.a.m.e.vent. Aponeurosis 3a is broad and strong, inserting posterior and medial to Aponeurosis 3, on the dorsal edge of the mandible.

Other woodpeckers examined—including *Picumnus*—are very similar in all respects. M.a.m.e.caud. is somewhat reduced in *Campephilus malherbi.*

M. pseudotemporalis superficialis

The origin is fleshy, and often also aponeurotic from the posterior wall of the orbit. Insertion is made via a narrow tendon on the dorsal medial surface of the mandible. This typically lies lateral to the bulk of the muscle, whose fibres attach on it in unipinnate fashion. The relationship of the muscle to the course followed by the Vth (trigeminal) cranial nerve is of interest. Typically the nerve lies more or less lateral to the muscle, separating it from M. adductor mandibulae externus. In all the families considered here (with a slight modification in some jacamars and puffbirds) the tendon eventually passes medial to the nerve and inserts below it, though this is not so in all bird groups (e.g. some Charadrii; Burton, 1974*a*).

CORACIIFORMES

In most members of the order, the origin is mainly well to the lateral side of the orbit, and generally rather high. On the medial side there is usually a group of fibres originating considerably lower, but this only constitutes a small proportion of the bulk of the muscle. The Vth cranial nerve usually runs under the muscle towards its *medial* side (not lateral as in most birds), and is unusually near the dorsal surface by comparison with many other groups. The ramus pterygoidei and ramus mandibularis of the nerve typically run close alongside each other for a considerable distance in most members of this order, and the tendon of the muscle in many cases runs between them.

Alcedinidae. The muscle is long and narrow, and its fleshy region extends much further anteriorly than in the other families of the order. In *Alcedo atthis* and *Halcyon chloris* there is a high lateral origin with an aponeurosis along its medial edge from which fibres diverge forwards on each side, those on the medial side coming from a distinct medial lobe with a relatively low origin on the orbit. The Vth cranial nerve runs under this medial lobe. In *Clytoceyx rex* the medial and lateral lobes remain distinct for much of the length of the muscle, and each is bipinnate.

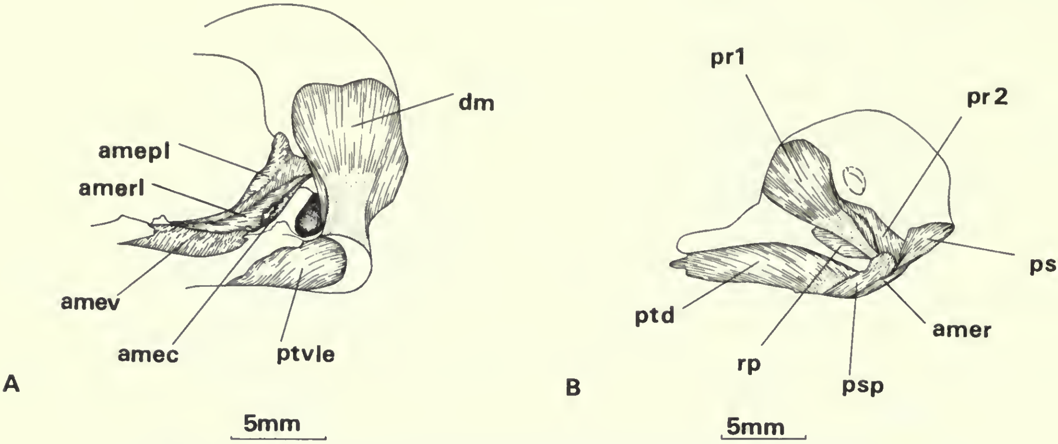

Fig. 14 *Upupa epops,* jaw musculature: A, lateral view; B, dorsal view.

TODIDAE. The muscle is small in size and elongated in shape. Most of its bulk originates fairly high in the orbit; a small region on the medial side originates lower than the rest. The Vth cranial nerve runs along the medial side of the muscle, separating it at the origin from M. protractor quadrati et pterygoidei. The muscle is unipinnate in structure, fibres inserting on a lateral aponeurosis. About level with the posterior end of M. pseudotemporalis profundus this aponeurosis merges with the long slender tendon of insertion.

MOMOTIDAE. The form of the muscle resembles that of the Todidae, but it is relatively considerably larger, the origin extending high up in the orbit. There is a distinct, though small, medial region with a much lower origin; this is bipinnate in *Momotus* and *Baryphthengus*, but of simple structure in *Electron*. The fibres of the muscle insert on an aponeurosis which cover the whole anterior surface of the muscle, merging into the tendon of insertion about level with the posterior limit of M. pseudotemporalis profundus. The Vth cranial nerve runs under the medial edge of the muscle.

MEROPIDAE. Similar to the preceding two families, but ranking between them in the relative size of the muscle and the dorsal extent of its origin. The medial region is very much reduced, and the muscle lies almost entirely lateral to the Vth cranial nerve.

LEPTOSOMATIDAE. The muscle resembles that of the Alcedinidae in form. It is long and narrow, and its fleshy region extends far forward. The lateral origin contributes less to the total bulk of the muscle than in other Coraciiformes. The posterior part of the muscle shows some bipinnate structure about a weak raphe attached to the orbit in the medial third of the muscle. The muscle is joined near its insertion by a slip from the lateral side of M. pseudotemporalis profundus. The Vth cranial nerve runs under the muscle towards its medial side.

CORACIIDAE. Similar to the Meropidae in form and situation, but the fleshy region extends further forward—to about the midpoint of M. pseudotemporalis profundus—in *Coracias benghalensis* and *Eurystomus glaucurus.* It is smaller, and the fleshy region more limited, in *Brachypteracias squamigera.*

UPUDIDAE. The muscle is bulky and less flattened than in the preceding families, and the Vth cranial nerve consequently lies much deeper. The lateral origin is well developed, and the fibres are attached in unipinnate fashion to a strong lateral aponeurosis which merges into the tendon of insertion about level with the posterior end of the short M. pseudotemporalis profundus.

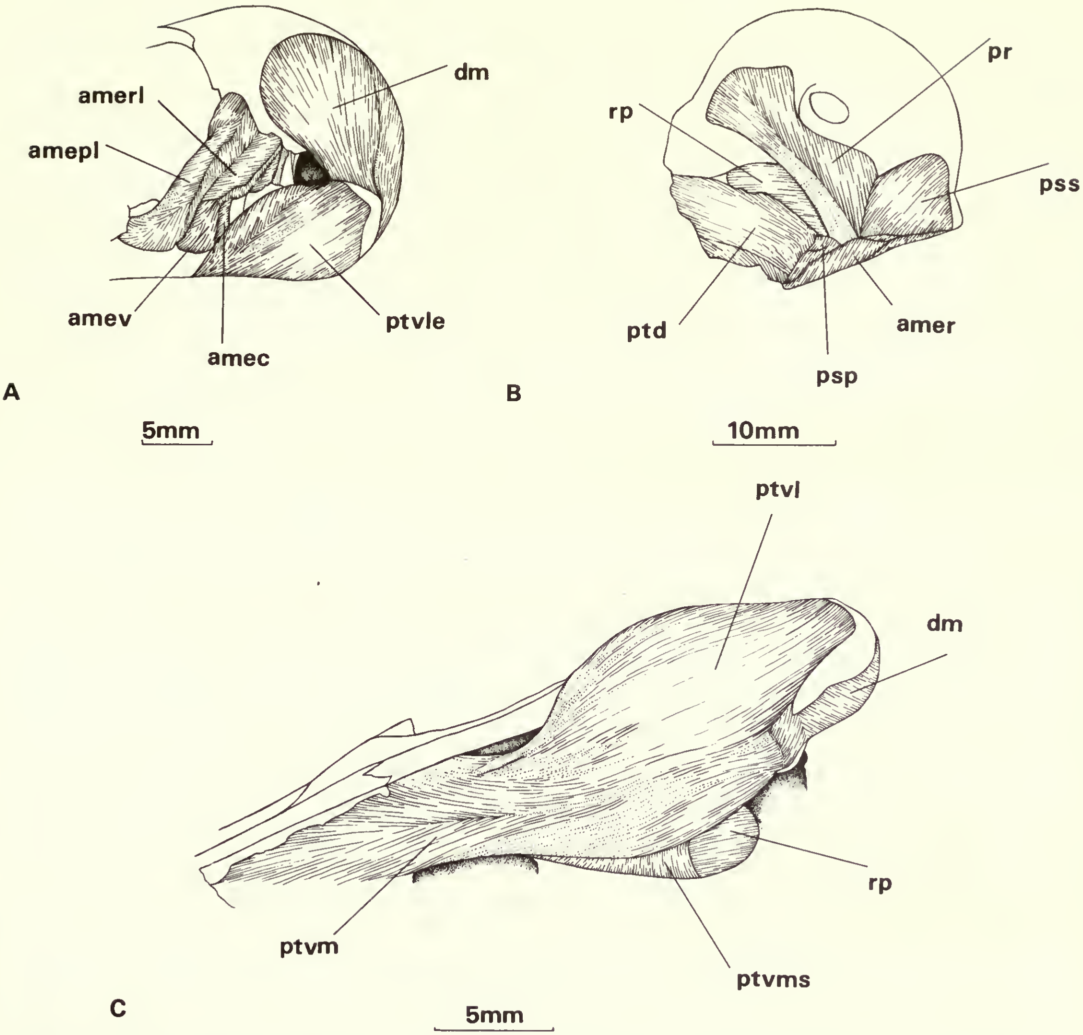

Fig. 15 *Phoeniculus purpureus,* jaw musculature: A, lateral view; B, dorsal view; C, ventral view.

PHOENICULIDAE. Very similar to *Upupa* in both species examined.

BUCEROTIDAE. Similar in form to that of the Upupidae and Phoeniculidae, but the medial edge is strongly emarginated by a crista on the wall of the orbit at about the junction of this muscle and M. protractor quadrati et pterygoidei.

PICIFORMES

The origin of M. pseudotemporalis superficialis is in general more medially situated than in the Coraciiformes, and never extends very high up the orbit wall. In many species the medial side of the muscle is produced as a narrow extension across part of the origin of M. protractor quadrati et pterygoidei. The fifth cranial nerve lies deeper than in most Coraciiformes (except in the Galbulidae and Bucconidae), and generally runs well towards the lateral side of the muscle. The ramus pterygoidei of the nerve usually turns mediad away from the ramus mandibularis after only a short distance, well posterior to the starting point of the muscle's tendon of insertion (except in the Galbulidae, Bucconidae and Picidae).

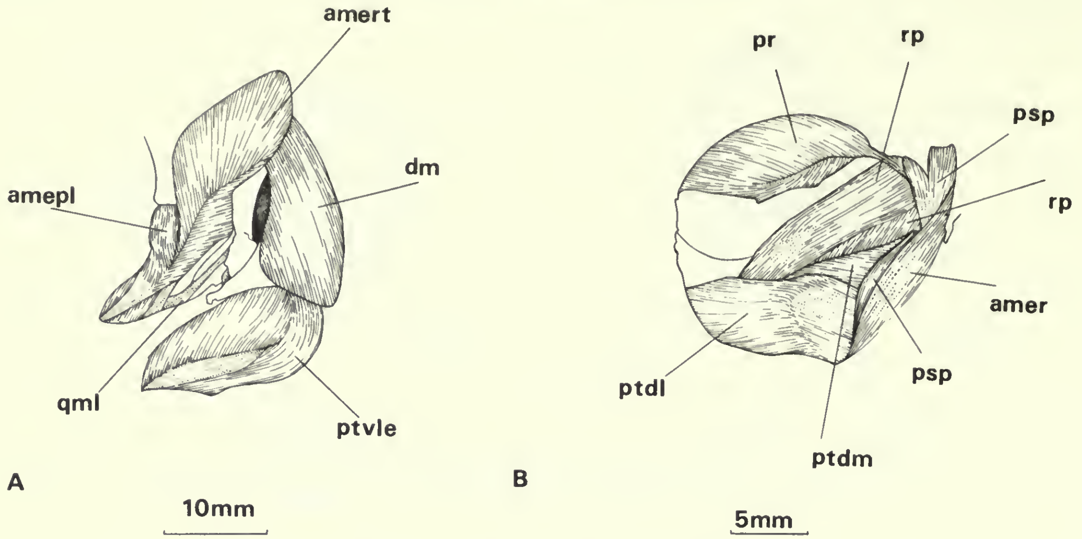

Fig. 16 *Tockus erythrorhynchus,* jaw musculature: A, lateral view; B, dorsal view.

GALBULIDAE. The muscle is vestigial in most jacamars, and entirely absent in one specimen of *Jacamaralcyon.* In this vestigial condition, it consists of a very small and narrow fleshy slip attached low on the orbit wall, immediately lateral to the fifth cranial nerve which, as in the Coraciiformes, lies superficial, with the ramus pterygoidei and ramus mandibularis running close together for some distance. A long and extremely slender tendon beginning level with the posterior end of M. pseudotemporalis profundus runs approximately between the ramus pterygoidei and ramus mandibularis of the nerve to insert just below the latter. In *Jacamerops* the tendon is forked at the insertion, one fork passing above the nerve to its attachment. The muscle is best developed—but still very small—in *Galbalcyrhynchus.*

BUCCONIDAE. The muscle is also vestigial in the puffbirds, and entirely absent in all three specimens of *Nonnula.* In some species (*Notharcus macrorhynchus, N. tectus, Hypnelus, Malacoptila*), it is somewhat better developed, and approximately the shape of an equilateral triangle, though still very small. The form of the fifth cranial nerve, and its topological relations with the muscle are the same as in the Galbulidae. In *Monasa morphoeus* there is a forked insertion like that in *Jacamerops.*

CAPITONIDAE. M. pseudotemporalis superficialis is of moderate size, with its origin low on the orbit wall, extending medially to partially cover the origin of M. protractor quadrati et pterygoidei. The fifth cranial nerve lies deep on the lateral side of the muscle. The tendon of insertion begins about level with the midpoint of M. pseudotemporalis profundus.

The medial extension is particularly marked in *Megalaima haemacephala.* The muscle is bipinnate in *Lybius bidentatus,* the raphe arising from the origin; there is some fleshy insertion as well as tendinous, but all medial and ventral to the ramus mandibularis of the fifth cranial nerve. There is a strong bipinnate medial slip arising from a prominent crista on the orbital wall in *Semnornis,* with a fairly broad fleshy insertion, also medial and ventral to the nerve. A similar condition is seen in *Trachyphonus,* as noted by Starck and Barnikol (1954).

INDICATORIDAE. The muscle is similar in form to that of *Megalaima haemacephala,* with a long medial extension at the origin. It is slightly bipinnate in *I. indicator,* and strongly so in *I. maculatus* and *Melichneutes* in which the raphe arises from a prominent crista on the wall of the orbit. In *I. minor*, however, the muscle is of simple structure, with fibres

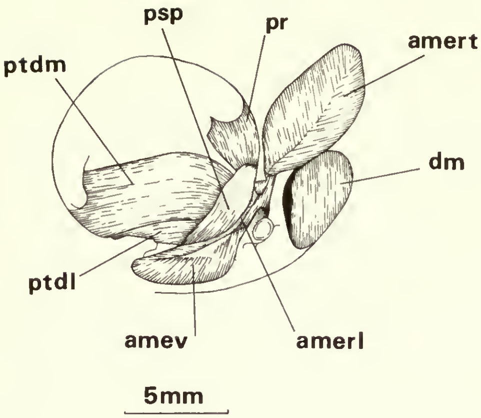

Fig. 17 *Galbula ruficauda,* jaw musculature, dorso-lateral view.

attached in a unipinnate arrangement on the lateral aponeurosis. The fifth cranial nerve, lies lateral to the muscle, and deep. The tendon of insertion begins well forward.

Ramphastidae. Bulky and bipinnate in the three species examined, but similar in general form to barbets. The raphe is in the medial third of the muscle, arising from a strong crista on the orbit wall. The fleshy part of the muscle extends far forward, and there is a small amount of fleshy insertion additional to the tendon. The fifth cranial nerve runs deep, roughly under the midline of the muscle.

Picidae. In *Jynx,* the muscle is of simple structure, with a long medial extension at the origin, much as in *Megalaima haemacephala.* In all Picinae and Picumninae examined, it is triangular in shape, and the origin is more lateral, with no medial extension. It is, however, of simple structure. The fifth cranial nerve runs under its midline.

M. pseudotemporalis profundus and *M. adductor posterior*
(N.A.A.: *M. adductor posterior = M. adductor mandibulae caudalis*)

These two muscles are closely associated, both functionally and morphologically, and it is convenient to treat them together. Like M. pterygoideus, they both act to lower the upper jaw at the same time that they raise the mandible. Since both attachments of each muscle move, the terms origin and insertion are arbitrary, but following usual practice they are considered as originating on the quadrate and inserting on the mandible. The origin of M. pseudotemporalis profundus is a fleshy one from the dorso-lateral surface of the orbital process of the quadrate, and often also from a dorsal aponeurosis attached to the medial edge of the process (generally rather a weak in the birds described here). It is otherwise largely a parallel-fibred muscle although a narrow band of fibres along the lateral or medial edges often shows a unipinnate arrangement.

The insertion is a wide fleshy one on the medial surface of the mandible; the muscle often overlaps the dorsal edge of the mandible to some extent. M. adductor posterior takes its origin from the proximal region of the orbital process and from the quadrate body. Lakjer (1926) regarded N. pterygoideus as separating this muscle from M. pseudotemporalis profundus, and his criterion is followed here, although Stark & Barnikol (1954) have suggested a different basis for discriminating the two. The insertion of M. adductor posterior is fleshy, and lies typically on the dorsal surface of the mandible, just posterior to the insertion of M.a.m.e.-caudalis, and to the medial surface of the mandible immediately dorsal to that of M. pterygoideus dorsalis medialis. However, in many species, there is more or less overlap onto the lateral surface of the mandible, ventral and posterior to the wide insertion of M.a.m.e.ventralis.

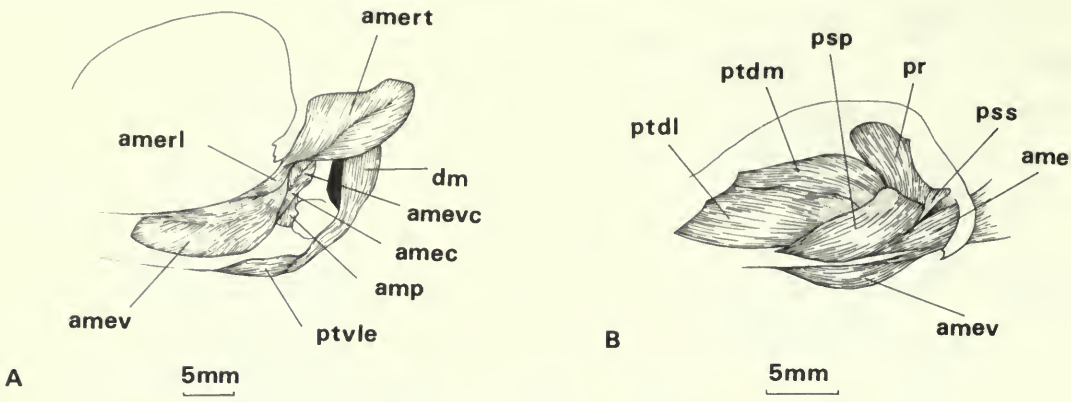

Fig. 18 *Monasa morphoeus,* jaw musculature: A, lateral view; B, dorsal view.

Alcedinidae. M. pseudotemporalis profundus is absent in all members of the Alcedininae and several species of Cerylinae. It is, however, present and reasonably well developed in all members of the Daceloninae, and appears particularly broad in *Dacelo gigas, D. leachii* and *Clytoceyx rex.* In the Cerylinae, the muscle is absent in all species of *Chloroceryle,* and in *Ceryle rudis.* It is present in *Ceryle torquata, C. alcyon* and *C. maxima*; no specimen of *C. lugubris* was available. In these species it is very small, with a narrow and largely aponeurotic attachment to the tip of the orbital process; it is very clearly separated from M. adductor posterior by N. pterygoideus and loose connective tissue. M. adductor posterior is of normal development in all the Alcedinidae, without extensions onto the lateral surface of the mandible. In members of the Cerylinae lacking M. pseudotemporalis profundus there is a vestigial, thin orbital process, and the origin of M. adductor posterior extends right to its tip; the identity of the more medial fibres is in no doubt, because they are all clearly traversed by N. pterygoideus. In the Alcedininae, the orbital process is virtually absent, and the origin of M. adductor posterior is consequently limited to the quadrate body.

Todidae. M. pseudotemporalis profundus appears fairly broad in dorsal view, but there is little indication of a dorsal aponeurosis. M. adductor posterior is fairly bulky and just visible laterally under M. adductor mandibulae externus caudalis.

Momotidae. M. pseudotemporalis profundus and M. adductor posterior are of similar relative development to those of the Todidae in *Momotus* and *Baryphthengus.* In *Electron,* M. adductor posterior shows a slight extension onto the lateral surface of the mandible, with a faint aponeurosis at its posterior edge.

Meropidae. M. pseudotemporalis profundus is fairly wide, and of even width as seen dorsally. Its dorsal aponeurosis is best developed in *Nyctiornis*, where there is a slight indication of bipinnate fibre arrangement anteriorly. M. adductor posterior is invisible in lateral view.

Leptosomatidae. M. pseudotemporalis profundus is relatively small and narrow. From the lateral edge of the medial tip of the orbital process of the quadrate arises a narrow slip which runs outward to fuse with M. pseudotemporalis superficialis near its insertion. M. adductor posterior is barely visible in lateral view.

Coraciidae. M. pseudotemporalis profundus is wide at the origin, tapering anteriorly to a rather narrow insertion. Its dorsal aponeurosis is well developed. M. adductor posterior is almost totally concealed in lateral view.

Upupidae. M. pseudotemporalis is small and narrow with a weak dorsal aponeurosis, and M. adductor posterior invisible laterally.

Phoeniculidae. Similar to Upupa, but M. pseudotemporalis profundus rather better developed.

BUCEROTIDAE. *Tockus erythrorhynchus.* M. pseudotemporalis profundus is relatively small, and its dorsal aponeurosis is weak. However, it shows a marked bipinnate fibre arrangement about a raphe arising on the orbital process. M. adductor posterior is concealed in lateral view.

GALBULIDAE. M. pseudotemporalis profundus is fairly small, and M. adductor posterior is barely visible laterally.

BUCCONIDAE. In most puffbirds, the medial edge of the post orbital process is long, and M. pseudotemporalis profundus is very wide, as viewed dorsally. It is probably best developed in *Nystalus* spp. An exception is *Hypnelus bicinctus,* in which it is relatively much narrower, and the medial edge of the orbital process is shorter than in other members of the family. M. adductor posterior is invisible laterally in all species.

CAPITONIDAE. M. pseudotemporalis profundus is fairly broad in most species although the dorsal aponeurosis is generally weakly developed, apparently least well developed in *Trachyphonus vaillantii.* M. adductor posterior has a small extension onto the lateral surface of the mandible in *Psilopogon pyrrholophus, Semnornis* spp., *Gymnobucco pelli* and *Pogoniulus leucolaimus;* the extension is a moderately large one in *Capito niger,* lying ventral and posterior to M. adductor mandibulae externus caudalis.

INDICATORIDAE. *Indicator indicator.* M. pseudotemporalis profundus is narrower than in most barbets. M. adductor posterior can be seen laterally under M.a.m.e.caudalis.

RAMPHASTIDAE. M. pseudotemporalis profundus is similar in form and development to most barbets in *Selenidera maculirostris.* In *Ramphastos toco* it appears narrow dorsally, especially at the insertion, but is deep nevertheless. M. adductor posterior is just visible laterally in both.

PICIDAE. In all species examined, including *Jynx,* M. pseudotemporalis profundus is of moderate size, and M. adductor posterior rather small, and invisible laterally.

M. pterygoideus

General structure. Lakjer (1926) recognized four principal divisions of this complex muscle, and his system is followed here. In most of the species examined, the aponeuroses of the muscle correspond closely to those described by Zusi (1962) and Burton (1974) for various Charadriiformes, and these are numbered according to Zusi's system. M. pterygoideus normally has its origin on the palatine and pterygoid, and inserts on the posterior part of the mandible. In some birds, a slip from this muscle inserts on the basitemporal plate of the skull. This slip, at one time referred to as 'M. retractor palatini', is considered under (5) below:

(1) *M. pterygoideus dorsalis lateralis.* (M.pter.dors.lat.) This division of the muscle is typically intimately connected with M. pterygoideus ventralis lateralis, and the two were thus treated as a single unit by Zusi (1962) and Burton (1974*a*). Fibres assigned to M.pter.dors.lat. are those originating on the dorsal surface of the palatine. They insert on the medial surface of the mandible immediately anterior to those of M. pterygoideus dorsalis medialis. The insertion is a broad and fleshy one; an additional surface for insertion is usually provided by a dorsal aponeurosis (Ap. M).

(2) *M. pterygoideus ventralis lateralis* (M. pter. vent. lat.). Origin is from the lateral edge and caudo-lateral tip of the palatine, usually via a strong aponeurosis (Ap. A^1). This aponeurosis generally extends some way across the ventral surface of the muscle, and is often fused with Ap. A_2 (see (4)). Its medial edge is commonly infolded, marking the boundary with M. pterygoideus ventralis medialis, and acting as a raphe, from which fibres of M. pterygoideus ventralis diverge caudad.

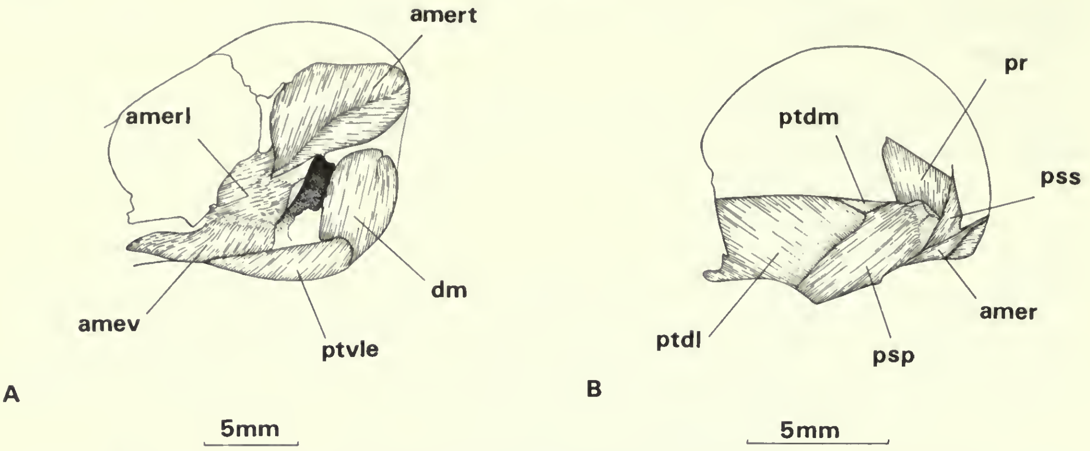

Fig. 19 *Trachyphonus darnaudii,* jaw musculature: A, lateral view; B, dorsal view.

The insertion of M.pter.vent.lat. is fleshy, around the ventral edge of the mandible, and commonly on its lateral surface as well. The laterally inserting fibres form a distinct lobe referred to as the 'venter externus' of the muscle (Hofer, 1950).

(3) *M. pterygoideus dorsalis medialis.* (M. pter. dors. med.) Origin is principally from the pterygoid, but commonly includes the caudal tip of the palatines. The origin is fleshy, and often aponeurotic as well, and the insertion, at the base of the internal process of the mandible, is fleshy, and also via a dorsal aponeurosis (Ap. O). Fibres originating on the antero-lateral face of the pterygoid and on the palatine diverge from those originating on the postero-medial face of the pterygoid. These two areas of the muscle are termed, respectively, M.pter.dors.med.anterior and M.pter.dors.med.posterior by Richards and Bock (1973). The anterior section is usually much the bulkier of the two. M.pter.dors.med. is separated from M.pter.dors.lat. by a groove, or sometimes a clear gap, into which, in most birds, the ramus pterygoideus of the Vth cranial nerve posses. In some species, the groove is absent, and the lateral and medial parts of M. pterygoideus dorsalis are continuous, as are Aponeuroses M and O.

(4) *M. pterygoideus ventralis medialis.* (M. pter. vent. med.). The ventral surface of the palatine provides the main surface for the origin of this division of the muscle; there is usually also a strong aponeurosis (Ap. A_2) attached to the palatine at the anterior boundary of the muscle and continued back some way across its ventral surface. The insertion, on the anterior face of the internal process of the mandible, is partly fleshy, but also includes a strong aponeurosis (Ap. N) attached to the medial tip of the process, and running into the muscle as a raphe. The fibres of M.pter.vent.med. are oriented more nearly parallel to the long axis of the skull than those of the rest of the muscle.

(5) *Retractor palatini slip.* Attachment of part of M. pterygoideus to the basitemporal plate has been reported in the Psittaciformes (Hofer, 1950; Burton, 1974*c*), Columbiformes (Didunculus; Burton, 1974*c*), Trogoniformes (Burton, 1974*c*), Bucerotidae (Starck, 1940) and many passerines (Möller, 1930, 1931; Engels, 1940; Fiedler, 1951; Bock, 1960*b*, etc.). This is clearly a feature which has evolved independently in several lines, and it is therefore not surprising that the structure and origins of the slip vary considerably. It generally derives from part or all of M.pter.vent.med., but may also include fibres of M.pter.dors.med. (Bock, 1960*b*).

CORACIIFORMES

A number of radical modifications in the structure of M. pterygoideus occur in this order, of which the most noteworthy are the shift of part of the origin of M. pterygoideus

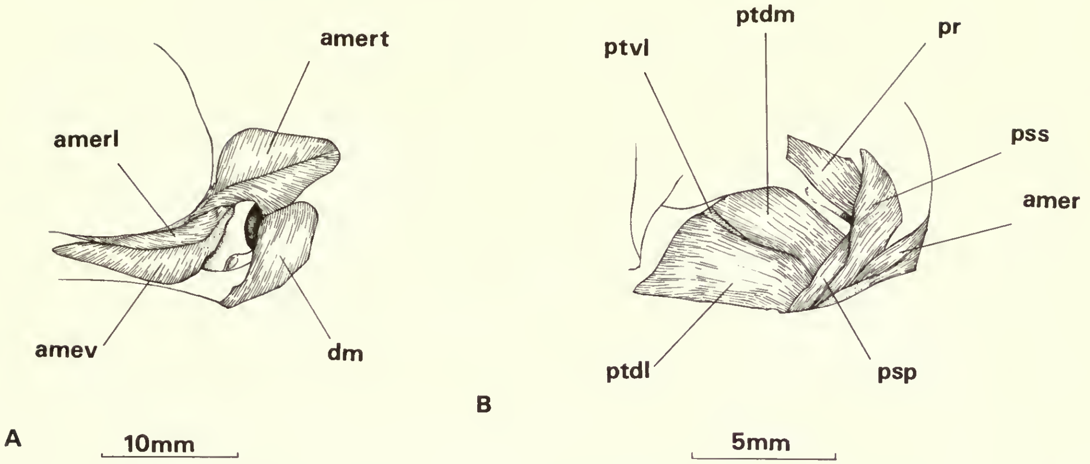

Fig. 20 *Indicator maculatus,* jaw musculature: A, lateral view; B, dorsal view.

lateralis to the maxillopalatine in the Alcedinidae, Phoeniculidae and Bucerotidae; and the development of a large retractor palatini portion in the Upupidae, Phoeniculidae and Bucerotidae.

Alcedinidae. The structure of M. pterygoideus in the Kingfishers departs extensively from the general structure given above. In the descriptions which follow, M.pter.dors.lat and M.pter.vent.lat. are considered as a single unit, M. pterygoideus lateralis (M.pter.lat.) for purposes of clarity.

Alcedo atthis: The groove separating M.pter.dors.med. from M.pter.lat. is long, and is oriented at only a small angle (approx. 28°) to the midline of the skull. M.pter.dors.med. is continued far forward, to the anterior margin of the palatine, which is raised into a prominent crest. M.pter.lat. is attached to the palatine fleshily and by a medial aponeurosis to the antero-dorsal crest and the dorsal surface anterior to this. The rest of its attachment is made via a lateral extension of the ventral aponeurosis (ap. A1) to the dorsal surface of the palatal mucosa near the rictus; and to the transverse flange on the ventral surface of the maxilla which marks the posterior limit of the internal ramphotheca of the upper jaw. There is also a small amount of fleshy attachment at the medial tip of the maxillo-palatine. M.pter.lat. is of bipinnate structure. The raphe (which runs approximately along the mixline of the muscle) arises from a very strong aponeurosis attached to the lateral surface of the mandible along the dorsal margin of the well developed venter externus; this aponeurosis also gives rise to the dorsal aponeurosis, Ap. M. The raphe is continued, weakening, to the anterior end of the muscle which is forked. The medial fork consists of fibres arising medial to the raphe, and it is this fork which provides the attachments on the palatine and maxillopalatine. The lateral fork, consisting of fibres arising lateral to the raphe, provides the attachments on the palatal mucosa and maxilla via Ap. 1.

The orientation of M.pter.dor.med. is nearly the same as that of M.pter.vent.med.—a contrast to the majority of birds in which the fibres of the two run at a sharp angle to one another. Consequently the two are largely fused in *Alcedo.* The most distinct part of M.pter.vent.med. is the medial region arising on the posterior edge of the pterygoid, and attached on the medial tip of the internal process of the mandible. The rest of the muscle arises by a short aponeurosis from a limited area at the posterior end of the ventral surface of the palatine, and is continuous with M.pter.dor.med. above it, its origin being an extensive fleshy one on the dorsal surface of the palatine. The combined M.pter.med. is bipinnate about the horizontally oriented raphe Ap. N, fanning out from the medial tip of the internal process of the mandible. Ap. N is situated in the dorsal quarter of the muscle.

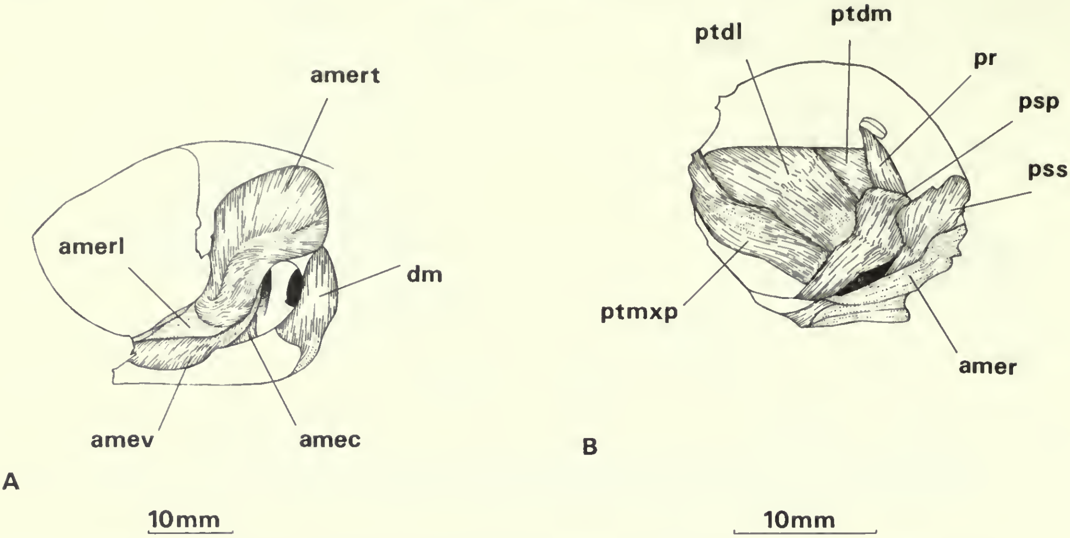

Fig. 21 *Selenidera maculirostris,* jaw musculature: A, lateral view; B, dorsal view.

The structure of M. pterygoideus in *Alcedo* may be thus summarized:

M. pterygoideus lateralis: *Origin:* Fleshy and aponeurotic on the antero-dorsal crest of the palatine, the medial tip of the maxillo-palatine, the palatal mucosa and the ventral surface of the base of the maxilla. *Insertion:* fleshy and aponeurotic on the lateral surface of the mandible (venter externus) and a limited region of the ventro-medial surface of the mandible near the base of the internal process. *Structure*: bipinnate about a raphe arising on the lateral surface of the mandible.

M. pterygoideus dorsalis medialis: *Origin:* fleshy on the dorsal surface of the palatine. *Insertion:* on the internal process of the mandible, fleshily and via. Ap. N.

M. pterygoideus ventralis medialis: *Origin:* mainly aponeurotic from the ventral surface of the palatine, and fleshy from the posterior edge of the pterygoid. *Insertion:* fleshy and via Ap. N on the internal process of the mandible. *Structure:* M.pter.dors.med. and M.pter.vent.med. form a unit which is bipinnate about Ap. N.

Other Alcedinidae: M.pter.lat. is of bipinnate structure in all members of the family examined except *Tanysiptera galatea.* The raphe runs roughly along the midline of the muscle in the Cerylinae and Alcedininae, but is shifted more or less to the lateral side in the Daceloninae. The attachment to the maxillo-palatine is small in the Alcedininae, and limited to its medial tip, while in the Cerylinae it is absent altogether. In the Daceloninae, however, this attachment is much more extensive, reaching an extreme in *Dacelo* (especially *D. novaeguinae* and *D. leachii*), *Melidora* and *Clytoceyx rex.* In these species, the attachment is broad, extending over much of the length of the maxillo-pallatine, and is made by a dorsal aponeurosis on the posterior edge of the maxillo-palatine, and fleshily on its ventral surface. The attachment to the palatine in these species is extremely limited, and takes the form of a narrow slip, its fibres diverging rostro-mediad from those attached to the maxillo-palatine. The main raphe of M.pter.lat. in *Dacelo, Clytoceyx* and *Melidora* lies lateral and ventral to its position in other kingfishers, so that the remainder of the muscle, attaching on the mucosa and maxilla via Ap. A1 is largely hidden by the more bulky section originating on the maxillo-palatine. In *Tanysiptera galatea* the attachment to the maxillo-palatine is present, and about as well-developed as in most *Halcyon* spp., but the attachment to the mucosa and maxilla is entirely absent.

M.pter.dors.med. extends to the antero-dorsal crest of the palatine in all kingfishers examined. The groove between this muscle and M.pter.lat. makes a relatively small angle

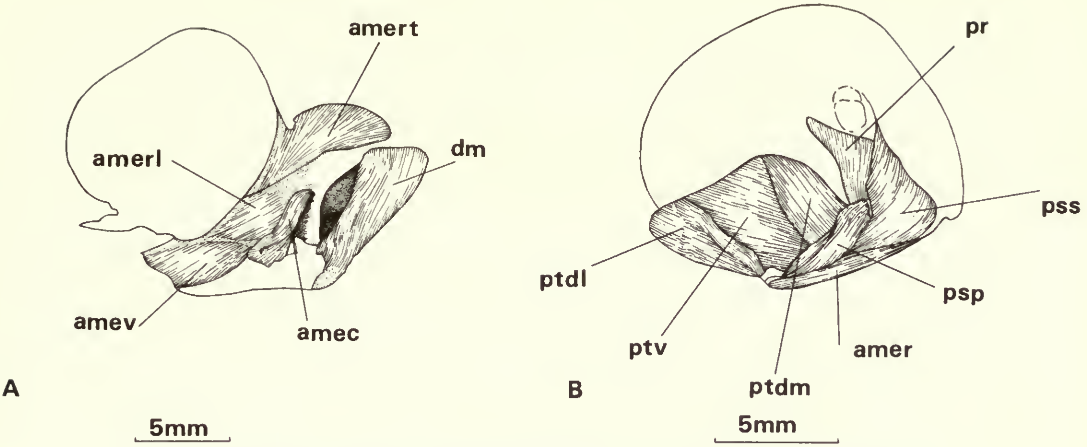

Fig. 22 *Jynx torquilla,* jaw musculature: A, lateral view; B, dorsal view.

to the midline of the skull in all Alcedininae and also Cerylinae (e.g. *Chloroceryle amazona,* 26°). However, among the Daceloninae, the groove is more steeply angled to the midline (i.e. more 'normal') in *Halcyon* and *Tanysiptera* (e.g. 35°, *Halcyon pileata;* 33°, *Tanysiptera galatea*)—in part a consequence of the relatively shorter pterygoids and more posteriorly situated palatines in the Daceloninae. In these genera, the distinction between M.pter.dors.-med. and M.pter.vent.med. is clearer, as a result of the different orientation of their fibres. Nevertheless, despite similar skull morphology, *Dacelo* and *Clytoceyx* show the smallest angle of groove to midline of all (approx. 22°—23° in both genera), due to the shift of much of the origin of M.pter.lat. from the palatine to the maxillo-palatine.

In all other features, M. pterygoideus conforms closely to the description for *Alcedo atthis* throughout the Alcedinidae.

Todidae. *Todus viridis.* M.pter.dors.lat. is of simple structure, with fibres converging evenly from the origin to the insertion near the base of the internal process of the mandible. M.pter.-dors.med. has origin only from the posterior end of the palatine and the groove separating it from M.pter.dors.lat. is oriented at about 40° to the midline of the skull. The ventral surface of M.pter.vent.med. shows a slight separation of fibres originating on the medial crest of the palatine, and those arising from its ventral surface. There is scarcely any venter externus of M.pter.vent.lat.

Momotidae. *Momotus momota.* M.pter.dors.lat. is bipinnate, with the raphe well over to the lateral side; part of its origin is on the dorsal surface of the palatal mucosa, lateral to the palatine. M.pter.dors.med. has little attachment on the palatine, and the groove separating it from M.pter.dors. lat. is steeply angled to the midline (approx. 50°). From the ventral aspect. M.pter.vent.med. shows marked separation into a lobe originating on the medial crest of the palatine, and that originating on the rest of the palatine. Most attachment of M.pter.-vent.lat. is at the base of the internal process, including the very strong Ap. M. The venter externus is well developed.

Baryphthengus ruficapillus is very similar. In *Electron platyrhynchum,* however, M.pter.-dors.lat. is of simple structure, and the groove separating it from M.pter.dors.med. runs further anterior, at an angle of about 33° to the midline.

Meropidae. *Nyctiornis amicta.* M.pter.dors.med. extends forward to the antero-dorsal crest of the palatine: the groove separating it from M.pter.dors.lat. is oriented at approx. 30° to the midline. M.pter.dors.lat. itself is of simple structure, and its area of insertion is mainly at the base of the internal process of the mandible. There is hardly any development of the venter externus. Ventrally, M.pter.vent.med. bulges out laterally, ventral to Ap. A1.

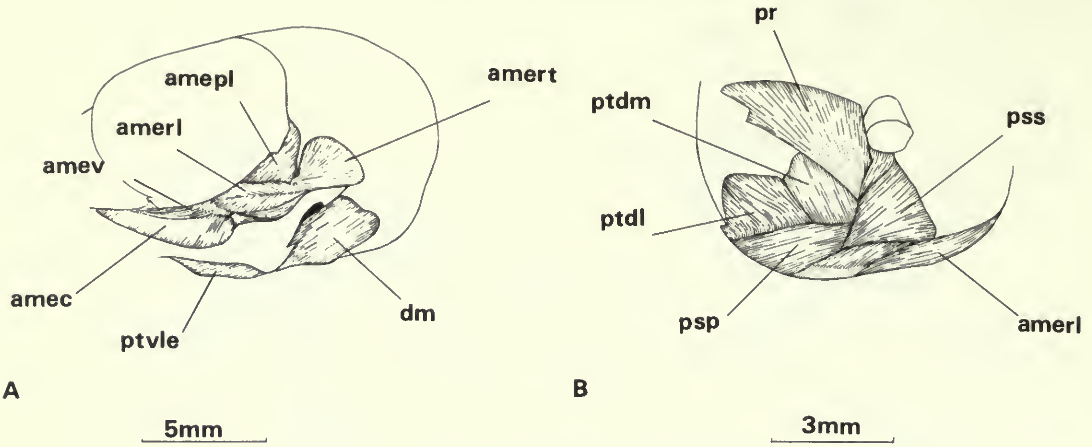

Fig. 23 *Sasia abnormis*, jaw musculature: A, lateral view; B, dorsal view.

Aerops albicollis is similar, but M.pter.dors.med. has even more extensive origin on the palatine, and is clearly broader and more bulky than M.pter.dors.lat. The groove between the two runs at approx. 26° to the midline.

Leptosomatidae. Dorsally, no clear groove can be distinguished separating M.pter.dors.lat. and M.pter.dors.med. Both are of simple structure, with fibres converging evenly towards the insertion low on the medial surface of the mandible, and at the base of the internal process. M.pter.vent.lat. has a moderately developed venter externus.

Leptosomatidae. M.pter.dors.med. is much reduced. There is a distinct posterior section as in the Coraciidae, and this is the only part of the muscle reaching the basiphenoid rostrum; the anterior section has origin only on the posterior half of the pterygoid, and is concealed by M. pseud.prof. in dorsal view. M.pter.vent.lat. has a small venter externus.

Coraciidae. *Coracias benghalensis*. M.pter.dors.med. extends well forward on the palatine, not quite reaching its antero-dorsal crest. The groove separating it from M.pter.dors.lat. is oriented at the relatively shallow angle of 35° to the midline. Fibres of M.pter.dors.med. originating on the postero-medial surface of the pterygoid are angled nearly parallel to the midline, forming a distinct posterior section. There is little development of a venter externus, and the insertion of M.pter.vent.lat. includes the medial surface of the mandible, as well as the base of the internal process. Ap. M. is inserted quite high on the medial surface of the mandible.

In *Eurystomus glaucurus* and *Brachypteracias squamigera*, M.pter.dors.med. also shows a distinct posterior section, but has little attachment on the palatine. The groove between this and M.pter.dors.lat. is steeply angled to the midline (49° in *Eurystomus*, 44° in *Brachypteracias*). There is no venter externus in *Eurystomus*, but a well developed one in *Brachypteracias*.

Upupidae. *Upupa epops*. There is no groove or other indication of demarcation between M.pter.dors.lat. and M.pter.dors.med. The pterygoid ramus of the 5th cranial nerve enters the muscle in a very posterior position immediately level with the anterior edge of the orbital process of the quadrate. The lateral fibres of M.pterygoideus dorsalis have a substantial area of insertion on the medial surface of the mandible, anterior to the base of the internal process, and the insertion of M.pter.vent.lat. includes a well developed venter externus. The posterior region of M.pter.dors.med. and the medial region of M.pter.vent.med. are modified to form a large retractor palatini portion, with substantial fleshy attachment on the basitemporal plate. The retractor palatini fibres arise partly on the medial half of the ventral surface and on the medial crest of the palatine; and also on the postero-medial edge (including part of the dorsal surface) of the pterygoid. The part arising on the pterygoid is bulky, and is prominent in dorsal view. The lateral half of M.pter.vent.med. is of normal structure, arising mainly on the lateral half of the ventral surface of the palatine, and inserted on the internal process of the mandible, with a raphe (Ap. N) fanning out from the medial tip of the internal process.

PHOENICULIDAE. *Phoeniculus purpureus.* As in *Upupa,* there is no separation of lateral and medial parts of M.pter.dors. This muscle is, however, strongly bipinnate, the raphe running in its outer quarter, roughly parallel to its lateral edge. The raphe is continuous medially with Ap. N, and dorsally with Ap. M. Ap. N. has an extended region of attachment to the mandible in the form of a crista along the dorsal edge of the anterior face of the internal process. The origin of M. pterygoideus dorsalis extends a long way forward, and its anterior edge is attached fleshily and by a dorsal aponeurosis to the whole ventral edge of the maxillo-palatine. M.pter.vent.med. also has a long area of origin on the ventral surface of the palatines, and there is a thin superficial band of fibres running from the groove between M.pter.vent.med. and M.retractor palatini to the mucosa in the midline. (Fig. 9c, ptvms). Other features, including the structure of M. retractor palatini, resemble *Upupa epops. P. aterrimus* resembles *P. purpureus*, but M.pter.dors. is not bipinnate, though attached to the maxillo-palatine. The venter externus is bulky, with a strong lateral aponeurosis which has a group of fibres attached in unipinnate fashion along its dorsal edge. *Rhinopomastus cyanomelas* shows attachment of M.pter.dors. to the maxillo-palatine, but as in *P. aterrimus,* the muscle lacks bipinnate structure. The venter externus is rather weaker than in the two previous species, with no obvious lateral aponeurosis or pinnate structure.

BUCEROTIDAE. *Tockus erythrorhynchus.* M. pterygoideus dorsalis is divided into lateral and medial parts by a clear groove running at approx. 40° to the midline of the skull. The pterygoid ramus of the Vth cranial nerve enters M.pter.dors.med. some way posterior to the groove, rather than passing into the groove itself as in all other birds considered in this study (except those showing no separation of medial and lateral parts). M.pter.dors.med. has an origin confined to the anterior edge of the pterygoid, but the retractor palatini portion of the muscle has an extensive dorsal origin including not only the posterior edge of the pterygoid, but also the medial edge of the posterior end of the pterygoid. The retractor palatini is pinnate in structure, with the raphe arising on the posterior tip of the palatine. The raphe is visible on the lateral face of the dorsal attachment of the muscle, fibres dorsal to it running more or less parallel with it, while those ventral to it diverge forwards to attach on the pterygoid.

M.pter.dors.lat. is weakly bipinnate about a broad dorsal aponeurosis (Ap. M.). Anteriorly there is an extensive fleshy origin along the whole length of the maxillo-palatine. M.pter.-vent.lat. has an extremely bulky venter externus, bulging out prominently on the lateral surface of the mandible. M.pter.vent.med., apart from the retractor palatini portion, is of normal structure, with a strong raphe (Ap.N).

PICIFORMES

The main departures from the general description are seen in the Galbulidae, in which M. pterygoideus lateralis shows extreme reduction; and in the Capitonidae and Ramphastidae, in which attachment of M.pter.dors.lat. to the maxillo-palatine is found.

GALBULIDAE. *Galbula dea.* M.pter.dors.lat. and M.pter.vent.lat. form a single unit which is greatly reduced in size by comparison with other birds. It consists of a narrow slip originating via Ap. A1 along the lateral edge of the palatine, and inserted on the ventro-medial and ventral edge of the mandible at the base of the internal process. In dorsal view, the groove separating M.pter.lat. from M.pter.dors.med. is oriented at the very narrow angle of 10° to the midline of the skull. M.pter.dors.med. extends appreciably further forward on the palatine than M.pter.lat. The pterygoid ramus of the Vth cranial nerve enters the muscle through

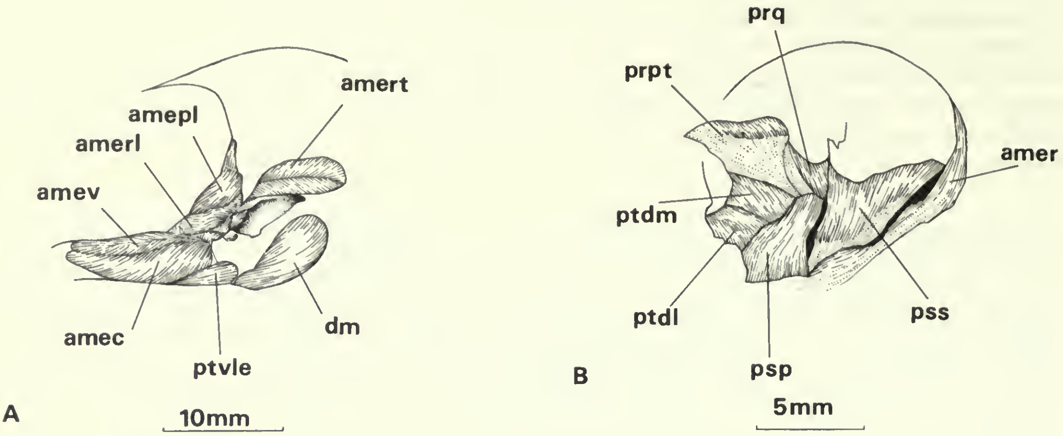

Fig. 24 *Dendrocopos major,* jaw musculature: A, lateral view; B, dorsal view.

the groove near the orbital process of the quadrate in the normal way. The remainder of the muscle is of normal structure.

In *Jacamerops aurea* there is a partial groove extending across the antero-medial half of the M.pter.dors.med. well back, and oriented at approx. 30° to the skull midline. M.pter.lat. is least reduced in *Galbalcyrhynchus leucotis,* in which the groove separating it from M.pter.dors.med. is angled at 15° to the midline.

Bucconidae. *Chelidoptera tenebrosa.* M. pterygoideus dorsalis is of normal structure, with the groove separating lateral and medial parts situated well back, and angled at 45° to the skull midline. M.pter.dors.med. extends only onto the posterior end of the palatine. Ventrally, M.pter.vent.med. shows marked separation between fibres originating on the main ventral surface of the palatine, and those originating on the medial crest, which pass superficial to the main part of the muscle. M.pter.dor.lat. inserts low, on the ventral edge of the mandible. The venter externus is very small.

In all other Bucconidae examined, M.pterygoideus dorsalis shows an approach to the Galbulidae, with M.pter.dors.med. extending further onto the palatine, and the groove separating it from M.pter.dors.lat. oriented much more parallel to the skull midline than in Chelidoptera. In most species, the groove is noticeably curved, its posterior quarter or so being more steeply angled to the midline than the rest. Extremes are reached in *Notharcus macrorhynchus* and *N. tectus,* and in *Nonnula ruficapilla,* in which the angle of the groove to the midline is approx 20° over most of its length, and M.pter.dors.med. reaches the antero-dorsal crest of the palatine, and is noticeably larger than M.pter.dors.lat. Less extreme angles, and smaller extensions of M.pter.dors.med. onto the palatine are seen in, e.g. *Hypnelus ruficollis* (approx. 30°), *Malacoptila panamensis* (27°), *Monasa morphoeus* (26°), *Nystalus chacuru* (25°). In *Nystalus chacuru, N. radiatus* and *N. maculatus,* M.pter.dors.lat is weakly bipinnate about a broad dorsal aponeurosis derived from Ap. M. The venter externus is weakly developed throughout, and entirely absent in *Hypnelus ruficollis* and *Nonnula ruficapilla.*

Capitonidae. *Megalaima haemacephala.* M.pter.dors.med. is very narrow, and situated far back, its boundary with M.pter.dors.lat. angled at 55° to the skull midline. Its origin nevertheless includes substantial attachment to the posterior end of the palatine. M.pter.dors.lat. is of simple structure, but its anterior end has attachment, fleshily and by a short, weak dorsal aponeurosis, to the medial 2/3 of the ventral edge of the maxillo-palatine. There is no venter externus. M.pter.vent.med. is of normal structure.

In most other barbets examined, M.pter.dors.med. is relatively larger, and extends further forward, the angle to the midline of its boundary with M.pter.dors.lat. ranging from 45° (*Trachyphonus vaillantii*) to 35° (*Pogoniulus leucolaima, Gymnobucco pelli*).

The extent and mode of attachment to the maxillo-palatine shows interesting variation. No attachment was found in *Psilopogon pyrrholophus, Gymnobucco pelli, Trachyphonus vaillantii* or *Capito niger.* In *Lybius bidentatus* there is a small amount of attachment on the ventral surface of the maxillo-palatine. In *Megalaima virens* there is a distinct attachment, but occupying rather less of the maxillo-palatine than in *M. haemacephala.* In *Pogoniulus leucolaima* the attachment is made by a distinct, if narrow, dorsal slip. The attachment is best developed in *Semnornis frantzii* and *S. ramphastinus.* In both species there is a distinct and well developed dorsal slip attaching on the medial half of the ventral edge of the maxillopalatine, fleshily and by a strong dorsal aponeurosis. Lateral to the slip, the origin of the muscle extends onto the dorsal surface of the palatal mucosa, near the rictus. In *S. rhamphastinus* there is a narrow band of fibres lateral to Ap. M and diverging forward from it in unipinnate fashion.

INDICATORIDAE. *Indicator indicator.* M. pterygoideus shows no unusual modifications, although extending well forward on the dorsal surface of the palatine, there is no attachment to the maxillo-palatine. M.pter.dors. is clearly divided into lateral and medial portions by a groove running at approx. 47° to the skull midline. The origin of M.pter.dors.med. is confined to the pterygoid (see p. 355 regarding structure of the pterygo-palatine junction in this family and the Picidae). M.pter.dors.lat. is bipinnate, with the raphe in the lateral fifth or quarter of the muscle. M.pter.vent.lat. and med. are of normal structure, and there is no venter externus. M.pter.dors.lat. is scarcely bipinnate in *I. maculatus,* and not all in *I. minor. Melichneutes* resembles *I. indicator.*

RAMPHASTIDAE. *Selenidera maculirotris.* M.pter.dors.med. is narrow, and situated well back, its boundary with M.pter.dors.lat oriented at 45° to the skull midline. M.pter.dors.lat. itself has an extensive attachment to the whole ventral edge of the maxillo-palatine in addition to its origin on the palatine. This attachment is made by a bulky raised dorsal slip, fleshily, and by a strong dorsal aponeurosis. The slip overlaps the lateral part of the palatine origin on its medial side. Beneath it lies a separate thin sheet of fibres with origin on the dorsal surface of the mucosa round the rictus, fleshily, and by a ventral aponeurosis (an extension of Ap. A1). There is scarcely any development of a venter externus. The rest of the muscle is of normal structure. *Ramphastos toco* is similar, but the slip originating on the maxillo-palatine is relatively even broader. The groove separating lateral and medial parts of M.pter.dors. is absent.

PICIDAE. *Jynx torquilla.* M.pter.dors.med. is narrow, and separated by a gap of about 10° from M.pter.dors.lat. The midline of this gap is oriented at about 65° to the skull midline. The origin of M.pter.dors.med. is confined to the pterygoid. Otherwise, the muscle shows no unusual modifications, and M.pter.dors.lat. is of simple structure. M.pter.vent.lat. and med. are of normal structure; there is no venter externus. *Dendrocopos major* has a strikingly elongated M.pter.dors.lat., extending forward almost to the midpoint of the nostril. This has a narrow band of fibres lateral to Ap.M., diverging forwards in a unipinnate arrangement. It is separated by a groove oriented at 40° to the skull midline from M.pter.dors.med., which has its origin confined to the pterygoid. There is no maxillo-palatine attachment or other unusual features. M.pter.vent.lat. and med. are of normal structure, and there is a moderately developed venter externus. Other woodpeckers examined are similar. In *Picumnus olivaceus* M.pter.dors.lat. is somewhat shorter, and of simple structure; otherwise, M.pterygoideus resembles that of the Picinae.

M. protractor pterygoidei et quadrati.

This muscle originates from the interorbital septum and the posterior wall of the orbit, medial to M. pseudotemporalis superficialis. Its insertion is on the dorsal surface of the posterior end of the pterygoid, and on at least the region of the quadrate body immediately adjacent to the pterygoid; there is frequently also insertion on the postero-medial surface of the orbital process. In some birds, the regions of the muscle originating on the interorbital septum and the posterior orbit respectively show more or less differentiation into two distinct parts. In such cases, the part originating on the septum is referred to as 'M. protractor 1', and that arising on the posterior orbit as 'M. protractor 2'. The insertion of M. protractor 1 is a narrow one on the dorso-medial surface of the posterior end of the pterygoid, and is partly made via an aponeurosis; that of M. protractor 2 is wider and fleshy, on the quadrate body and usually also the postero-medial surface of the orbital process. The lateral fibres of M. protractor 2 may pass dorsal to the insertion of M. protractor 1. Medial fibres of M. protractor 2 may attach on the aponeurosis of M. protractor 1 in a pinnate arrangement.

ALCEDINIDAE. The muscle is narrow in form, but relatively fairly large. It shows no differentiation into parts 1 and 2, and has no attachment to the orbital process, which is in any case vestigial or absent in the Alcedininae and several Cerylinae.

TODIDAE. M. protractor is well developed, and its origin on the orbittum and interorbital septum is high. It shows slight differentiation into two parts, but there is only limited attachment to the orbital process, low down, near its base.

MOMOTIDAE. M. protractor is narrow, its origin extending high on the orbit and interorbital septum. It has no attachment to the orbital process. In *Baryphthengus* it shows slight bipinnate structure, but there is no real differentiation into two parts.

MEROPIDAE. M. protractor is large, and has insertion over the entire medial surface of the orbital process. However, it shows no differentiation into two parts.

LEPTOSOMATIDAE. The muscle is relatively rather small, but has extensive attachment to the orbital process. There is no clear division into two parts.

CORACIIDAE. M. protractor is relatively small. It has attachment to the postero-lateral half of the orbital process, but shows no differentiation.

UPUPIDAE. M. protractor is extremely large, its origin extending high, and nearly to the anterior end of the orbit. It is differentiated into two parts; part 1 is surrounded near its insertion by a strong aponeurosis, which is strongest along the posterior edge and partly ossified in some specimens. Fibres of part 1 run ventrally and posteriorly to their attachment on this aponeurosis, and fibres of part 2 run ventrally and anteriorly to attach to its other side in a strongly bipinnate arrangement. There is, however, no attachment to the orbital process.

PHOENICULIDAE. Similar to Upupa, but part 1 extends rather less far forward, especially in *Rhinopomastus.* Parts 1 and 2 are even further differentiated in *Rhinopomastus,* lateral fibres of Part 2 passing across the dorsal side of Part 1 at its insertion, but as in *Phoeniculus,* there is no attachment to the orbital process.

BUCEROTIDAE. M. protractor is quite small, and shows no differentiation or attachment to the orbital process.

GALBULIDAE. The muscle is fairly large, but generally of simple structure; there is an indication of differentiation into two parts in *Galbalcyrhynchus* and *Jacamerops.* There is attachment to the full length of the orbital process.

BUCCONIDAE. The development of M. protractor varies considerably. It appears to be best developed in *Hypnelus bicinctus,* in which the origin extends high on the interorbital septum, and there is a distinct division into parts 1 and 2. Part 2 is attached over most of the orbital process except the medial half of its medial edge. It is attached to the entire medial surface of the orbital process in *Nonnula ruficapilla,* although there is no differentiation into two parts. It is well developed also in *Chelidoptera,* and somewhat less so in *Nystalus.* In *Notharcus, Malacoptila* and *Monasa,* M. protractor is relatively small, and has little attachment on the orbital process.

CAPITONIDAE. M. protractor is generally narrow, and of simple structure, with no attachment to the orbital process. In *Psilopogon,* its aponeurosis appears particularly well developed along its anterior edge, and fibres insert on it in unipinnate fashion.

Indicatoridae. Very similar to most Capitonidae.

RAMPHASTIDAE. Similar to the Capitonidae.

PICIDAE. In *Jynx.* M. protractor resembles that of the Capitonidae. It is narrow and fairly small, with no subdivision or attachment to the orbital process. In the remaining members of the family, including *Picumnus*, the muscle is greatly enlarged, and clearly divided into two parts, and attached to the entire medial surface of the orbital process. Part 1 attaches high and far forward on the interorbital septum. Its insertion is by a very strong aponeurosis arising from a long spur on the pterygoid. Part 2 arises from the posterior orbital wall; some of its medial fibres insert on the aponeurosis of Part 1, but most on the orbital process. In some, the area for insertion is slightly increased by a small aponeurosis extending medially from the tip of the orbital process, and merging with the aponeurosis of Part 1.

M. depressor mandibulae

This muscle is fairly small, and of uniform structure throughout the species examined, with the exception of the Upupidae and Phoeniculidae. In general, it originates from the exoccipital and insects over a wide area on the posterior end of the articular, including the posterior surface of the internal process of the mandible. Both origin and insertion are mainly fleshy. In the birds examined here, surface aponeuroses are in most cases only moderately or weakly developed. They occur on the dorsal surface of the muscle (arising from the ventral edge of the exoccipital) and near the insertion, on the lateral and central surfaces (arising from the lateral and ventral edges of the posterior face of the articular).

In the Upupidae and Phoeniculidae, the muscle is much larger than in the other families studied, extending at the origin well up onto the temporal region of the squamosal. The area for insertion is increased by the development of a long retroarticular process—a backward extension of the articular, continued some distance posterior to the internal process. Only the medial face of the retroarticular process is occupied by M. depressor, whose fibres run rostro-lateral to meet it. Lateral and dorsal aponeuroses are well developed, but show no infolding or internal branches as in, e.g. the Huia (Callaeidae, *Heteralocha acutirostris;* see Burton 1974*b*) and some Charadrii (Burton 1974*a*). However, in the Phoeniculidae, some ventral fibres pass under the edge of the lateral aponeurosis and insert in a narrow band along the ventral border of its lateral surface. The only other family showing any approach to the Upupidae and Phoeniculidae is the Bucerotidae. In this family, although the muscle shows no marked enlargement, there is a definite indication of a retroarticular process, the postero-ventral corner of the articular projecting backwards, rather than being emarginated as in all the remaining families.

Tongue and hyoid apparatus

Although the morphology of the horny tongue has been described for a number of Coraciiform and Piciform birds (e.g. in Beddard, 1898), anatomical details of the hyoid skeleton and musculature are largely lacking, except in the case of the Picidae (Leiber, 1907*a* & *b*). Nomenclature used in descriptions largely follows that of Bock (1972) and Richards & Bock (1973) N.A.A. equivalents (Baumel *et al.* 1979) are given where they differ from terms used here.

Tongue

The horny tongue varies greatly among the families studied. Extreme tongue reduction is seen in the Alcedinidae, Upupidae, Phoeniculidae and Bucerotidae. Very long tongues are

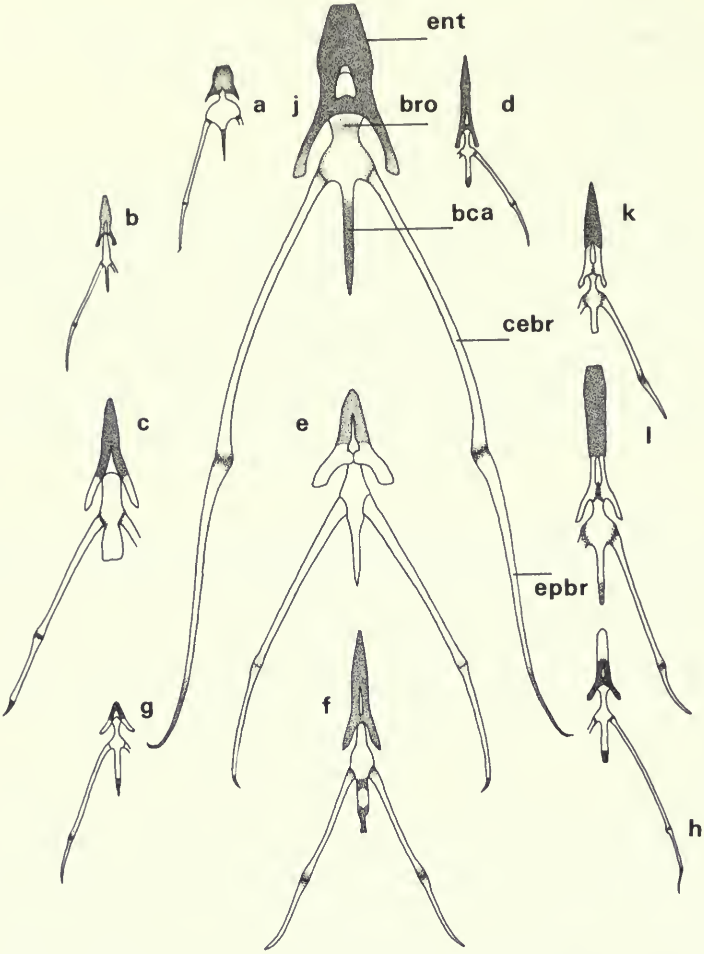

Fig. 25 Hyoid skeletons of Coraciiformes and Galbuloidea. Cartilage revealed by bulk staining with New Methylene Blue is indicated by stippling. (a) *Alcedo atthis*; (b) *Todus todus*; (c) *Momotus momota*; (d) *Aerops albicollis*; (e) *Leptosomus discolor*; (f) *Coracias benghalensis*; (g) *Upupa epops*; (h) *Phoeniculus purpureus*; (j) *Buceros bicornis*; (k) *Galbula dea*; (l) *Monasa morphoeus*.

seen in several families, such as the Coraciidae (particularly the ground rollers), Momotidae, a few barbets and the Ramphastidae. In absolute values, the tongues of the larger toucans must rank among the longest of all birds.

The extraordinarily long and extensible tongues of the Picidae cannot be directly compared with those of other families, since much of their length is taken up by the greatly elongated basihyal, and part of the hyoid horns; the horny tongue itself is much reduced, though still a vital part of the feeding apparatus. Surveys of the varied morphology of woodpecker tongues and hyoid apparatus have been provided by Steinbacher (1934, 1935, 1941, 1955, 1957).

Brush tongues occur in several families. Brush structure is highly developed, involving both tip and more or less of the sides in most Momotidae and the Ramphastidae. The latter family show this feature in extreme form; the tongue of *Ramphastos toco,* for example is a remarkable and beautiful structure, delicately tipped and fringed with fine laciniae for 80% of its considerable length. The Coraciidae, especially the ground rollers, also have quite well

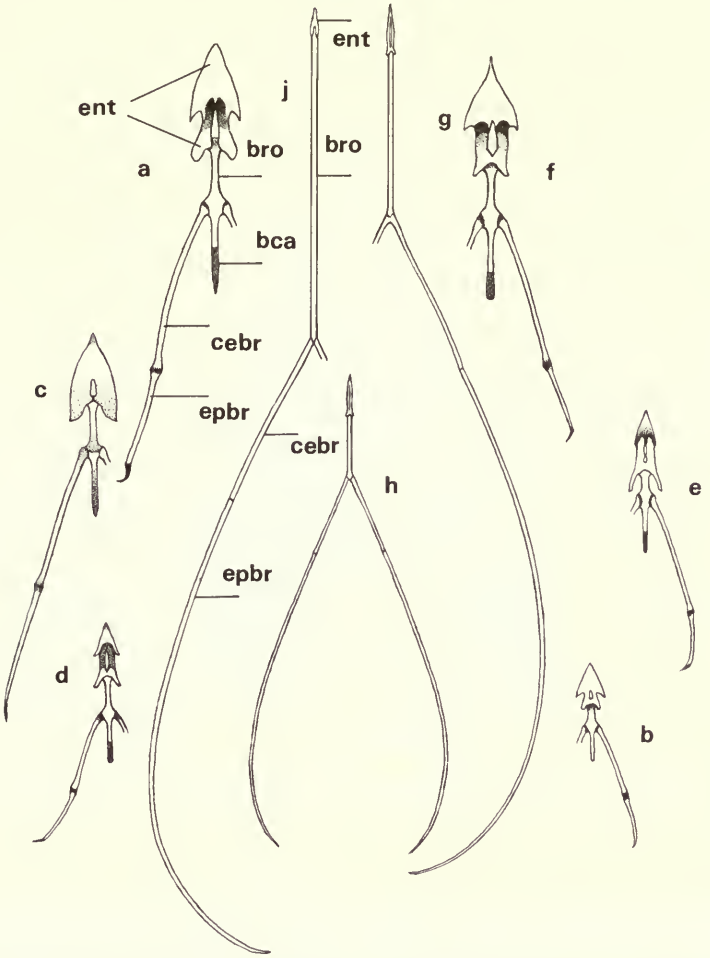

Fig. 26 Hyoid skeletons of Piciformes other than Galbuloidea. (a) *Psilopogon pyrolophus*; (b) *Pogoniulus bilineatus*; (c) *Lybius bidentatus*; (d) *Trachyphonus darnaudii*; (e) *Indicator indicator*; (f) *Selenidera maculirostris*; (g) *Jynx torquilla*; (h) *Sasia abnormis*; (j) *Colaptes auratus*.

developed brush tongues, and a moderate brush tip is also seen in *Capito* and *Semnornis* among the Capitonidae. Slight indications of brush structure at the tongue tip are seen in the Meropidae and *Jacamerops*. An African barbet (*Buccanodon melanolophus*) has a bifid tongue tip. Barbed tongues are characteristic of Picidae other than *Jynx*.

Apart from these, tongues are of simple structure for most of their length in all other species, that is to say, in the Alcedinidae, Todidae, Upupidae, Phoeniculidae, Bucerotidae, Bucconidae, Indicatoridae and most Galbulidae and Capitonidae. Basal barbs are normal as in most birds, but are particularly numerous in the Phoeniculidae and Bucerotidae, occurring on the dorsal surface as well as the margins in *Phoeniculus purpureus* and hornbills. Basal barbs are lacking in the Coraciidae, as noted by Beddard (1898). Many species show a slight indication of a median groove dorsally, corresponding with a ridge on the horny lining of the upper jaw, but a particularly strongly marked groove is characteristic of the Bucconidae, and quite noticeable also in *Jacamerops* and *Galbula* (Galbulidae).

Hyoid skeleton

The hyoid skeletons of representative species of each family are depicted in Figs. 19 & 20.

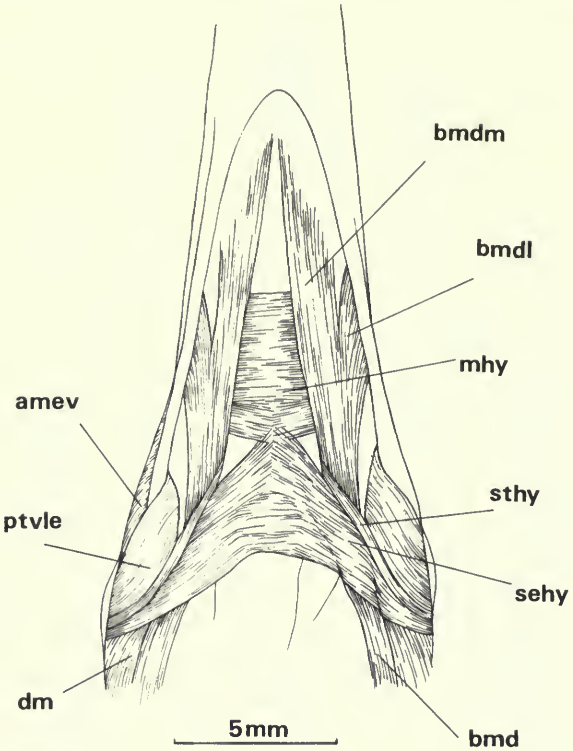

Fig. 27 *Todus todus.* Ventral view of superficial tongue muscles.

These illustrations eliminate much of the need for description; however, a few points deserve comment. The entoglossum generally tends to be more heavily ossified in the Piciformes than in the Coraciiformes, where any ossification is mainly confined to its posterior half. In general, the postero-lateral processes are longer in the Coraciiformes, producing more of an 'arrowhead' shape than in the Piciformes. The size of the entoglossum generally reflects the development of the tongue, but its form shows various features of interest in some Piciformes. The peculiar broadened tip of the entoglossum in *Monasa* is perhaps of minor significance; its sharply demarcated cartilaginous anterior and bony posterior much resemble the entoglossum of *Galbula.* Among the typical Piciformes, a more intriguing modification is seen; this takes the form of a strongly broadened anterior section, in some cases with backwardly directed lateral processes, as though an additional entoglossum had been grafted onto the front of the original. Of the Capitonidae checked for this feature, *Psilopogon* and *Trachyphonus darnaudii* showed it in a strongly developed form, and *Megalaima virens* moderately, while it was absent in *Lybius bidentatus.* Among other families, it is strongly developed in *Selenidera,* and moderately in *Indicator.* Within the Picidae, the entoglossum is very short and narrow, though with a slightly narrowed 'waist' posteriorly in *Jynx* and *Sasia.*

The basihyal is rather short and often broad in most Coraciiformes, and in the Galbulidae and Bucconidae. Broadening reaches an extreme in the Alcedinidae, where the basihyal is broader than long, forming a flat plate, with just a tiny narrow projection anteriorly to articulate with the entoglossom. The basihyal has well marked lateral flanges in the Todidae. In the Upupidae and Phoeniculidae, the basihyal has a characteristic 'hour-glass' form, also seen, though less strongly, in the Bucerotidae. In the typical Piciformes, the basihyal is

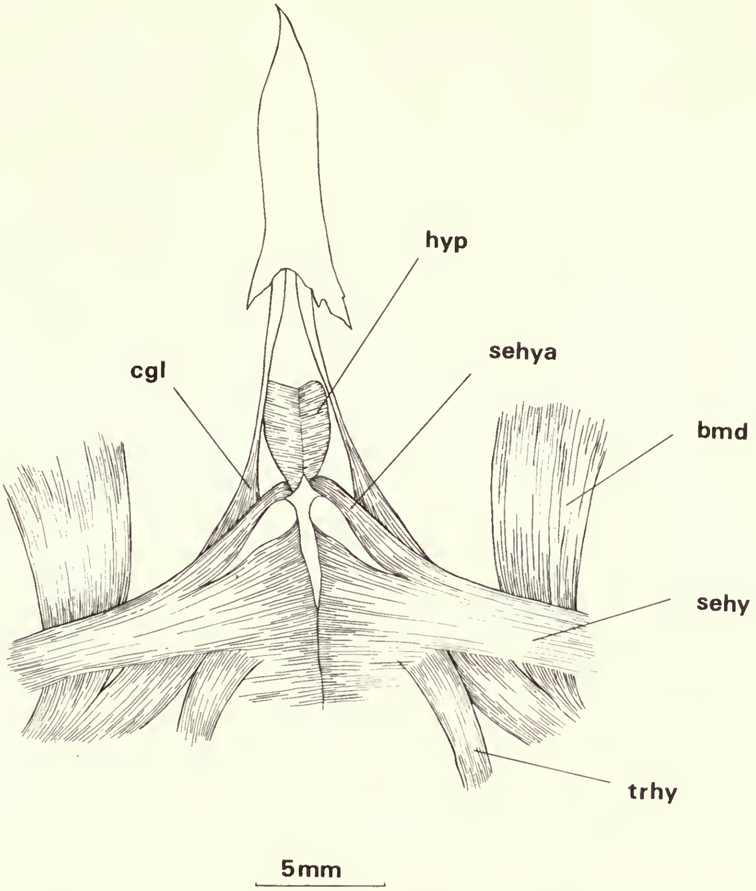

Fig. 28 *Coracias abyssinica.* Ventral view of tongue muscles to show anterior slip of M. serpihyoideus.

generally simple in shape, and rather long and narrow, reaching an extreme in the Picidae. *Pogoniulus* and *Indicator* are exceptions in which the basihyal is rather short.

Other parts of the hyoid skeleton require little comment. It may be noted that the great length of the hyoid horns seen in the Picidae has been attained mainly by elongation of the epibranchiale.

Hyoid muscles

M. mylohyoideus (N.A.A.: *M. intermandibularis*)
This very thin muscle is a sheet of fibres extending across the floor of the buccal cavity between the medial surfaces of the two mandibular rami, to each of which it is attached fleshily along a narrow line dorsal to M. branchio-mandibularis (and M. genioglossus where present). Its posterior end may merge with M. serpihyoideus. There appears to be no median raphe of insertion as in *Loxops* (Richards & Bock, 1973). The muscle is weakly developed in most of the families examined here, and was barely detectable in *Coracias benghalensis, Galbula dea* and *Megalaima haemacephala.* It appeared best developed in the Meropidae, *Indicator* and the larger Capitonidae. However, comparisons are rendered difficult by the varying states of contraction of the muscle in different specimens, resulting from the common practice of putting cotton wool plugs into the buccal cavity of specimens at the time of collection.

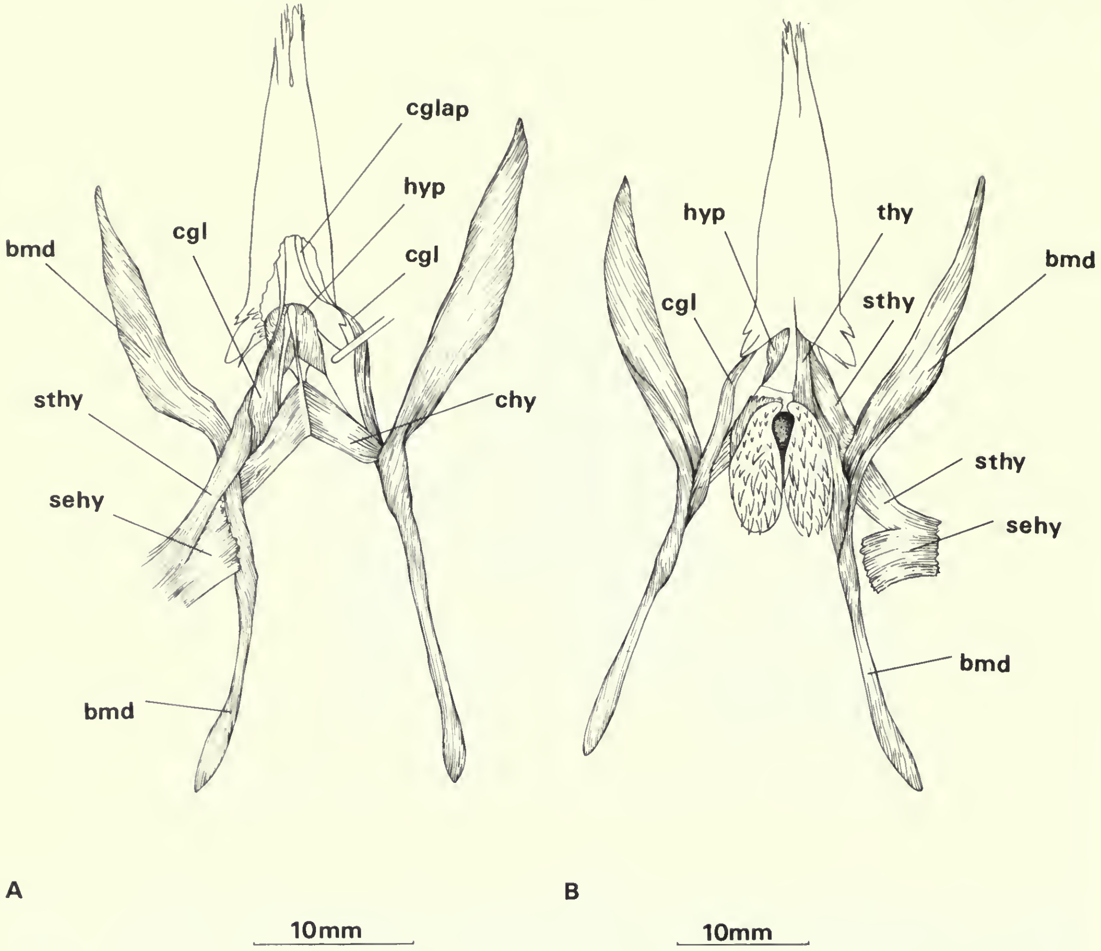

Fig. 29 *Megalaima zeylanica,* tongue musculature: A, ventral view; B, dorsal view. Left M. ceratoglossus free from basihyal and pinned aside.

M. ceratohyoideus (N.A.A.: *M. interceratobranchialis*)
The muscle originates fleshily on the ceratobranchiale close to its articulation with the epibranchiale. It passes along the ceratobranchiale, surrounded by M. branchiomandibularis, then diverges mediad to insert on a median raphe with M. ceratohyoideus from the opposite side. The insertion lies deep to M. serpihyoideus and M. mylohyoideus, and immediately ventral to the urohyal.

M. ceratohyoideus is absent in the Indicatoridae and Picidae, and feebly developed in the Alcedininae, in which insertion is on the posterior edge of the basihyal and anterior tip of the urohyal, rather than on the midline. Otherwise it shows little noteworthy variation among the species studied.

M. stylohyoideus
This muscle has a common fleshy origin with M. serpihyoideus on the postero-ventral edge of the mandible. It appears as a narrow slip which diverges from the anterior edge of M. serpihyoideus and runs to a fleshy insertion on the dorso-lateral surface of the basihyal, typically at its anterior end, and lateral to that of M. thyrohyoideus. This is its condition in the families studied here, with the following exceptions:

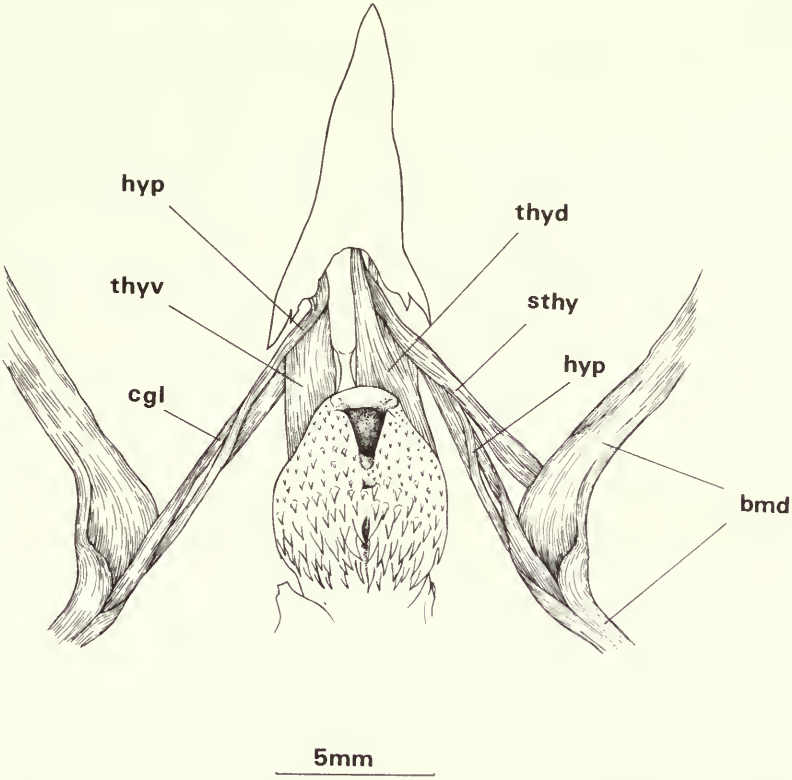

Fig. 30 *Indicator maculatus.* Dorsal view of tongue musculature to show M. hypoglossus obliquus.

ALCEDINIDAE. Insertion is on the dorsal surface of the anterior tip of the ceratobranchiale.

TODIDAE. M. stylohyoideus is extremely slender and absent in one specimen.

MOMOTIDAE. Insertion on the dorso-lateral surface of the posterior end of the basihyal.

CORACIIDAE, Galbulidae, Bucconidae: M. stylohyoideus is apparently replaced by a slip from M. serpihyoideus (q.v.).

UPUPIDAE. Extremely slender.

BUCEROTIDAE. Absent.

PICIDAE. Generally much reduced, with no attachment on the hyoid skeleton, and probably absent in some (see Leiber, 1907*a* & *b*).

M. serpihyoideus

Origin is on the postero-ventral edge of the mandible, medial to that of M. stylohyoideus. The insertion is on a medial raphe, the right and left muscles together forming a shallow, forwardly directed 'V'. The anterior tip is in close proximity to M. mylohyoideus posterior, and may merge with it. The muscle is similar in all the groups examined except the Coraciidae, Leptosomatidae, Galbulidae and Bucconidae. In these families, a narrow slip diverges from the anterior edge of the muscle (which is very narrow in *Leptosomus*) to insert around the ceratobranchiale–basihyal articulation. The insertion is in fact on the ventral surface of the anterior tip of the ceratobranchiale in all except *Eurystomus* and *Leptosomus*, in which attachment is on either side of the posterior ventral surface of the basihyal. Where M. stylohyoideus is absent (Coraciidae, Galbulidae, Bucconidae) this slip corresponds with it in origin, but is quite distinct in its completely ventral insertion, rather than a lateral or dorsal one. However, the presence of both this slip and a normal M. stylohyoideus in *Leptosomus* makes it clear that the slip is not just a M. stylohyoideus with altered insertion.

M. branchiomandibularis

In all birds previously studied, M. branchiomandibularis (=M. geniohyoideus) originates fleshily on the medial surface of the mandible just anterior to the venter externus of M. pterygoideus ventralis medialis (if present), and division at the origin into an anterior and a posterior portion is common. This is also its origin in some of the families investigated here, but a modified form of origin (either far anterior on the mandible, or from the ventral surface of the buccal mucosa) is seen in others. In this modified form, the muscle is flattened in the horizontal plane, whereas in its typical condition, flattening is less pronounced and oriented nearer to the vertical plane.

In all cases, insertion is fleshy on the distal part of the epibranchiale. The muscle is twisted around both ceratobranchiale and epibranchiale. M. branchiomandibularis is generally the largest tongue muscle, and in the Picidae reaches an enormous size due to the great elongation of the hyoid horns. Variations in the size and position of these horns are described by Steinbacher (1934 *et seq.*).

ALCEDINIDAE. *Alcedo*. Origin entirely on the medial surface of the mandible and extending far forward nearly to the mandibular symphysis. There is no clear division into two parts. The hyoid horns, and therefore the area of insertion, are short.

Other Alcedininae resemble *Alcedo*. In the Cerylinae, *Megaceryle* spp., *Chloroceryle amazona* and *C. inda* resemble *Alcedo*. *Chloroceryle americana* and *C. aenea* show great reduction of M. branchiomandibularis. The origin is limited to a small area on the ventral medial edge of the mandible, just anterior to the venter externus of M. pterygoideus ventralis medialis. In *C. aenea* the muscle is reduced to a tiny slip, and could almost be termed vestigial. In the majority of Daceloninae, origin on the mandible is limited to the anterior region near the symphysis, but there is additional origin from the ventral surface of the buccal mucosa. In these species, the origin of the muscle is flattened in the horizontal plane, rather than the more vertical one shown where the mandible is the main site of origin. In *Pelargopsis, Tanysiptera* and *Lacedo*, attachment appears to be mainly from the mandible, as in *Alcedo*; in *Halcyon saurophaga* it is almost entirely from the mucosa.

TODIDAE. In three specimens of *T. todus* the origin is divided into two clear parts. The bulkier part is attached partly on the medial surface of the mandible, but mainly on the mucosa, extending well anterior. The smaller part is a slip running close to the midline, left and right sides being in contact in some specimens. This medial slip resembles an M. genioglossus, but is distinguished by its insertion on the epibranchiale, to which it runs medially and dorsally relative to the main part. In a fourth specimen, the origin is undivided and confined to the mucosa.

MOMOTIDAE. *Momotus*. The origin of M. branchiomandibularis is not subdivided, and is mainly on the medial surface of the mandible, with a small amount of attachment to the mucosa anteriorly. The insertion is normal.

In *Baryphthengus,* the origin is roughly half from the mandible and half from the mucosa. In *Electron,* the mucosa is the main site of origin, with only a small amount of attachment to the mandible.

MEROPIDAE. Origin is largely on the mucosa, extending far anterior, with only a small area of attachment on the mandible. There is no obvious subdivision of the muscle.

LEPTOSOMATIDAE. The origin of M. branchiomandibularis is of typical form, confined to the medial surface of the mandible, and showing clear division into anterior and posterior portion.

CORACIIDAE. Origin mainly on the mucosa (entirely in *Coracias*), extending anteriorly nearly to the symphysis. No subdivision.

UPUPIDAE. Origin entirely on the mandible, but extending far anteriorly. No subdivision, and rather narrow.

PHOENICULIDAE. Similar to the Upupidae.

BUCEROTIDAE. Origin is from a bony ledge at the mandibular symphysis, and the muscle is narrow and flattened in the horizontal plane. In *Tockus erythrorhynchus,* the left and right muscles meet in the midline at the symphysis, lying superficial to the origin of M. genioglossus, which is also on this ledge. In *Buceros bicornis* and *Bucorvus leadbeateri,* the left and right muscles remain separate at the origin, and do not overlap M. genioglossus.

GALBULIDAE. Origin resembles that in the Bucerotidae, being mainly from a medially situated bony ledge at the mandibular symphysis, though with some attachment also to the mucosa. The left and right muscles do not quite meet at the midline, although there is no. M. genioglossus. The gap is widest in *Galbalcyrhynchus.* The muscle is narrow and horizontally flattened.

BUCCONIDAE. As in the Galbulidae, except that the narrow gap between right and left muscles is occupied by a well-developed M. genioglossus.

CAPITONIDAE. M. branchiomandibularis originates entirely from the medial surface of the mandible, and consists of a single portion.

INDICATORIDAE. As in the Capitonidae, but there is some subdivision into two portions.

RAMPHASTIDAE. As in the Capitonidae.

PICIDAE. Despite the enormous size of this muscle in the Picidae, its origin is basically a conventional one on the medial surface of the mandible, though extending from the anterior edge of M. pterygoideus ventralis medialis forward to the mandibular symphysis. M. geniothyreoideus (Leiber 1907*a* & *b*) is apparently a derivative of M. branchiomandibularis, originating anteriorly on the medial surface of the mandible, dorsal to M. branchiomandibularis, and inserting on the dorsal surface of the trachea, just posterior to the larynx.

M. genioglossus

This muscle is absent from many groups of birds, and where present, is often difficult to detect. Its origin is fleshy, or by a short aponeurosis, from the medial surface of the mandible, at or near the symphysis, and it runs along the ventral side of the buccal mucosa to insert in the region of the tongue base. It runs adjacent to a vein, and where poorly developed could well be confused with it. This vein is apparently a branch of the mandibular vein (Hughes 1934), joining it near the posterior end of the lower jaw. The vein appears to be present on the right side only in most of the families studied (both sides in *Alcedo atthis;* left side only in *Halcyon chelicuti*), but could not be traced in many specimens.

M. genioglossus was found in eight of the fifteen families investigated here, as follows:

MOMOTIDAE. Vestigial, left and right sides originating close together on the mandibular symphysis. It fades out short of the tongue base.

MEROPIDAE. Similar to the Momotidae; best developed in *M. pusillus.*

CORACIIDAE. Present in *Brachypteracias* spp., *Attelornis* and *Uratelornis,* and quite well developed. The origin is on the mandibular symphysis, where the right and left muscles unite. Insertion is on the ventral side of the mucosa lateral to the tongue base.

UPUPIDAE. A single, slender median muscle arising at the symphysis, and fading out on the mucosa just short of the tongue base. The site of origin is the ventral surface of a well developed bony ledge, level with the dorsal edge of the mandible.

PHOENICULIDAE. Origin is by a short aponeurosis from the symphysis, on a less distinctly marked bony ledge than in the Upupidae. The muscle is better developed and the right and left muscles unite only near the origin. Insertion is on the mucosa near the base of the tongue.

BUCEROTIDAE. A single median muscle, but very well developed. Origin is at the symphysis, from a more or less well marked bony ledge, shared also by M. geniohyoideus, which lies ventral (superficial) to M. genioglossus in *Tockus*, and lateral to it in *Bucorvus* and *Buceros*. Insertion is on mucosa near the tongue base in *Tockus*, but around the posterior end of the basihyale in *Bucorvus* and *Buceros*. The muscle is particularly bulky in *Bucorvus*.

BUCCONIDAE. Present throughout, left and right muscles having a combined origin on the symphysis, and insertion on the mucosa lateral to the tongue base.

RAMPHASTIDAE. A vestigial median genioglossus was found in *Selenidera*, with origin at the symphysis, but fading out on the mucosa short of the tongue base.

PICIDAE. M. geniothyreoideus, included here under M. branchiomandibularis could alternatively be a modified form of M. genioglossus—see discussion, p. 435.

M. ceratoglossus

In all birds so far studied, this muscle originates fleshily entirely on the dorso-lateral surface of the ceratobranchiale. It is a pinnate muscle whose short fibres insert on a lateral aponeurosis. This merges anteriorly into a strong tendon inserting on a tubercle on the ventral side of the posterior end of the paraglossale. The dorso-medial surface of the muscle is concave, to fit the ceratobranchiale.

In the families investigated here the extent of origin is the principal feature showing variation. The origin is from the entire length of the ceratobranchiale in the Todidae, Leptosomatidae, Coraciidae, Bucerotidae, Galbulidae, Bucconidae and Picidae. The muscle stops more or less short of the anterior tip of the ceratobranchiale in the Alcedinidae, Momotidae, Upupidae and Phoeniculidae. In the remaining families there is more or less attachment also to the basihyal. In the Indicatoridae there is a slight amount of attachment to the basihyal just at its articulation with the ceratobranchiale. In the Capitonidae, there is attachment along the entire ventro-lateral surface of the basihyal except in *Trachyphonus* (posterior half of basihyal and ceratobranchiale only) and in *Psilopogon* (origin only on ceratobranchiale). In the Ramphastidae, origin includes the full length of the basihyal.

M. ceratoglossus anterior and M. hypoglossus medialis

The small muscles at the base of the tongue have given rise to considerable confusion in the literature. The definitions followed here are those employed by Burton (1974*a*). M. ceratoglossus anterior is the name given to a small group of fibres arising from the tendon of M. ceratoglossus just before its attachment to the ventral surface of the paraglossale. These fibres insert partly on the entoglossum, but mainly on a strong median aponeurosis which runs the length of the ventral surface of the tongue. M. hypoglossus medialis is an unpaired median muscle arising on the anterior tip of the basihyal and inserting on the median aponeurosis.

Both muscles, together with their median aponeurosis, are absent in the majority of families studied here. M. ceratoglossus anterior is present in the Meropidae, in which it is very small, and the Leptosomatidae, in which it is well developed. In the Ramphastidae, fibres from the main part of the muscle extend onto the paraglossale, but there is no distinct ceratoglossus anterior, and no median aponeurosis. M. hypoglossus medialis is found in the Meropidae, Galbulidae and Bucconidae; it is well developed in the first, smaller in the second, and extremely small in the third.

M. hypoglossus obliquus

In all birds previously studied this muscle originates on or around the basihyale and inserts fleshily on the postero-lateral tip of the paraglossale. Two main forms occur; in Type 1 (Burton, 1974*a*), the right and left muscles merge in the midline, forming a continuous band of fibres which passes under the basihyale. In Type 2, the right and left muscles meet ventrally, but remain separate. In Type 1, the muscle is generally shorter than in Type 2, and confined to the anterior part of the basihyale.

Most of the Coraciiformes examined conform reasonably closely to one or other type. However, the Upupidae, Phoeniculidae and Piciformes (with the exception of the Galbulidae and Bucconidae) show a highly distinctive modification of Type 2, in which the right and left sides are entirely separate not even meeting ventrally and originate far back on the basihyale or in some also on more or less of the ceratobranchiale. In this modified form, the muscle is long and narrow, reaching an extreme in the Indicatoridae and Picidae, with its fibres oriented at only a small angle to the basihyale. This contrasts with its normal form, which is short and stout, the fibres being oriented at a large angle to the basihyale—90° in the case of the more anterior fibres.

ALCEDINIDAE. The muscle is of Type 2, but rather poorly developed, so that right and left sides usually fail to meet at the ventral midline, and leave the anterior half of the short basihyale exposed.

TODIDAE. Reasonably well developed, and of Type 1, completely covering the anterior half of the basihyale.

MOMOTIDAE. Type 2, completely covering the short basihyale.

MEROPIDAE. Type 2, but short, covering slightly less than half of the rather long basihyale.

LEPTOSOMATIDAE. Type 2, but short and rather small, covering slightly over half the short basihyale.

CORACIIDAE. Type 2, the left and right sides just failing to meet, but otherwise covering all of the short basihyale.

UPUPIDAE. The left and right muscles are completely separate, originating on the posterior basihyale, and the head of the ceratobranchiale; however the muscle is narrow and its total bulk is small, the basihyale being short.

PHOENICULIDAE. The two sides are quite separate, and origin is on the posterior basihyale, and the ceratobranchiale anterior to the origin of M. ceratoglossus. The muscle is somewhat shorter in *Rhinopomastus* than in *Phoeniculus*.

BUCEROTIDAE. The muscle is vestigial. The right and left muscles are separated by a wide gap, and their origin is confined to the anterior half of the basihyale. M. hypoglossus obliquus is completely concealed by the anterior fibres of the bulky M. ceratoglossus.

GALBULIDAE. Type 2, covering the entire basihyale.

BUCCONIDAE. Type 2, covering the entire basihyale.

CAPITONIDAE. The muscle is of Type 2, but long and narrow, with origin well back on the posterior half of the basihyale. The origin extends onto the anterior tip of the ceratobranchiale in *Pogoniulus*.

INDICATORIDAE. The muscle is very extensively developed, its origin including the posterior basihyale and the entire dorsal surface of the ceratobranchiale as far as its articulation with the epibranchiale. The origin is medial and dorsal to that of M. ceratoglossus. Insertion is by a strong, narrow dorsal aponeurosis, which extends back some distance into the origin, acting as the raphe of a bipinnate fibre arrangement.

RAMPHASTIDAE. The muscle is long and narrow, with an extensive origin on the posterior basihyale and anterior ceratobranchiale.

PICIDAE. From examination of *Jynx torquilla, Dendrocopos major* and *Picumnus olivaceus,* it seems quite clear that M. ceratoglossus superior, described by Leiber (1970*a* & *b*) in various Picidae, is in fact simply a very long M. hypoglossus obliquus. This point is considered in more detail in the discussion (pp. 417–418).

M. tracheohyoideus and M. tracheolateralis (N.A.A. terminology: see text)

These two muscles insert close together on the cricoid cartilage, and both run the length of the neck. M. tracheohyoideus arises on the sternum or clavicle, and runs lateral to M. tracheolateralis, adhering closely to the skin of the neck. M. tracheolateralis arises on the syrinx and runs along the ventro-lateral surface of the trachea.

The site of origin of M. tracheohyoideus is the clavicle in the Alcedinidae, Todidae, Momotidae, Meropidae, Leptosomatidae, Coraciidae, Upupidae, Phoeniculidae, Galbulidae and Bucconidae. The origin is usually a fairly wide fleshy one along a narrow line in the medial half or third of the anterior edge of the clavicle and right and left muscles remain separate. The origin is fleshy on the antero-ventral tip of the keel of the sternum or the clavicular symphysis in the Capitonidae, Indicatoridae, Ramphastidae and Picidae. This is generally a narrower origin than that on the clavicle and right and left muscles meet at the origin. In the Bucerotidae, both sites of origin are utilized, and the muscle forms an extensive sheet over most of the ventral side of the neck, closely adhering to the skin.

In most of the families considered here, M. tracheohyoideus inserts fleshily on the medial surface of the ceratohyal, near its anterior end, and on the dorso-lateral surface of the cricoid between the two heads of origin of M. thyrohyoideus. In the Indicatoridae, attachment to the ceratohyal is slight, and in the Capitonidae (except *Psilopogon*) and Ramphastidae it is absent altogether. The complex insertions of M. tracheohyoideus in the Picidae are thoroughly described by Leiber (1907*a* & *b*).

(According to Baumel *et al.,* 1979 (N.A.A., Systema respiratorium, Note 45), the muscle originating on the clavicle should be called M. cleidohyoideus and that arising on the sternum should be M. sternohyoideus. However, the evidence of this study (particularly the condition in the Bucerotidae) seems to indicate that both are derived conditions of the same muscle, and the common term of M. tracheohyoideus for both has been given preference. See also Part 3, p. 418).

M. tracheolateralis inserts on the ventral surface of the cricoid, medial to the ventral origin of M. thyrohyoideus. It appears to be absent in *Coracias.* In the Upupidae, M. tracheolateralis merges with M. tracheohyoideus, and they insert together on the ventral cricoid and the anterior tip of the ceratohyal.

M. thyrohyoideus (N.A.A.: *M. cricohyoideus*)
This muscle originates from the cricoid cartilage by ventral and dorsal heads. The ventral head arises from the ventral surface of the cartilage, and the dorsal head from its lateral surface. Insertion is on the dorso-lateral surface of the anterior end of the basihyale—typically medial and slightly posterior to the insertion of M. stylohyoideus if present.

Little variation was encountered among the forms studied here.

The neck and its musculature

The most important general account of the avian neck is that by Boas (1929), providing the foundation for all subsequent studies. The account of passerine cervical anatomy by Palmgren (1949) is also of great value. Detailed studies of small groups of species have been made by Zusi (1962), Zusi & Storer (1969) and Burton (1974*b*). While this paper was nearing completion, a detailed account for several Picidae was published by Jenni (1981).

Cervical vertebrae

Despite the wide range of feeding apparatus modifications shown by the head in the two orders, the cervical vertebrae are relatively uniform in their major features. Defined as vertebrae which bear either no movable ribs, or movable ribs not articulating with the sternum, there are either fourteen or fifteen (Beddard, 1898). The cervical vertebrae of birds fall into three fairly well defined sections, with different functional properties (Boas, 1929). Section I (the most anterior) can only be flexed downward, Section II only upward, and Section II. mainly downward, though anteriorly upwards as well. In the Coraciiformes and Piciformes, as in most birds studied, Section I usually consists of the first five vertebrae, 5 often appearing transitional, as in the Picidae; Boas (1929) gives a first section count of four for *Picus viridis.* Section II comprises vertebrae 6 to 9 or 10, and Section II the remainder. Descriptions of the morphological features which control the range of bending are given by Zusi & Storer (1969); although referring to a grebe (*Podilymbus*) possessing several more vertebrae than Coraciiform or Piciform birds, the structural modifications concerned are essentially similar.

Some noteworthy variations among the Coraciiformes and Piciformes may now be summarized. In Segment I, the first vertebra (the 'atlas') is, as in all birds, a simple ring of bone without a neural spine; in the Bucerotidae, it is fused with 2. Vertebrae 2 and 3 invariably

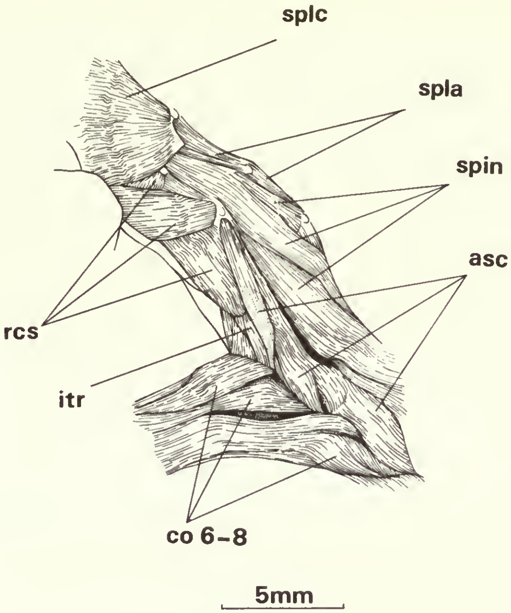

Fig. 31 *Alcedo atthis.* Superficial anterior cervical musculature. M. rectus capitis lateralis and ventralis and M. biventer cervics not shown. M. complexus freed from cranium and turned aside.

bear tall neural spines, and so often, does 4. Neural spines are continued further back, in some cases, and extend to 6 or 7 in the Alcedinidae, Phoeniculidae, some Capitonidae and Picidae. The spines normally decrease evenly in height from front to back, though in some woodpeckers there is actually an increase from 2 to 4, and then a steady reduction in height. A series of fused ribs is generally present from 3 or 4 onwards (5 in *Leptosomus* and *Upupa*), but these are reduced in the Bucerotidae and absent in the Picidae. Some anterior vertebrae may possess bony struts connecting the transverse process with the dorso-lateral crest, or the costal process with the lateral crest, or both. Exactly which vertebrae varies widely; the dorsal strut occurs most commonly on 3 and 4, the ventral on 5, 6 and 7. Only two species examined (*Phoeniculus purpureus, Colaptes auratus*) had a dorsal strut on 2, and only two had ventral struts posterior to 7 (*Phoeniculus purpureus,* on 8; *Upupa epops* on 8, 9 and 10). Dorsal and ventral struts occur together, if at all, usually only on 4, but *Nystalus chacuru* is remarkable for having both together on 5, 6 and 7.

Hypapophyses occur anteriorly and posteriorly, but are absent from the middle region of the neck. The anterior ones are usually found on vertebrae 2 to 4, though often on 2 to 3 only. That on 2 is often distinctly bifurcate, the two projections pointing backwards. Those on 3 and 4 may have a similar, but less pronounced shape. In the Picinae, very deep hypapophyses are found on 2 to 5. The ventral side of the atlas (1) also bears a hypapophysis like process, which is frequently bifurcate posteriorly. This provides insertion for M. flexor colli brevis, and is particularly strongly developed in the Picinae. Posteriorly, hypapophyses extend back into the thoracic region, starting usually on 9 or 10, but on 8 in *Jynx,* 11 in *Nyctiornis, Upupa* and *Selenidera,* and on 12 in *Tockus.* In the Picidae (other than *Jynx*), the subvertebral bridge which is present from 5 or 6 rearwards shows some indication of a hypapophysis on all vertebrae, but this is only well defined on 10 (the last vertebra with such a bridge) and vertebrae posterior to it. The subvertebral bridge in the Picidae has long been known (see, e.g. Beddard, 1898), but has apparently not been noted in other Piciform families. However, there is a complete subvertebral bridge on 8 in *Indicator,* with an incomplete bridge also on 6, 7 and 9. In *Jynx,* a subvertebral bridge is present only on 8 and 9.

Cervical muscles

Dissection of neck muscles is arduous and time consuming, and it was found impractical to examine the full range of species used in other parts of this study. The species actually investigated are referred to in appropriate places in the text, and group names are used only where an adequate range of species has in fact been dissected. For similar reasons, three muscles (Mm. splenius accessorius, Mm. intercristales and Mm. interspinales) have been omitted, while for some others (M. longus colli ventralis, Mm. intertransversarii and Mm. inclusi) the level of detail studied has been deliberately limited.

M. biventer cervicis

Origin is from the dorsal aponeurosis of M. spinalis in the region of 13, and the muscle inserts on the dorsomedial edge of the occipital deep to M. complexus. As its name implies, this muscle has two fleshy bellies, at origin and insertion, while the middle region of the muscle consists of a flat strap like tendon. The length of this tendon relative to the fleshy bellies varies considerably. The muscle is best developed in the Alcedinidae, in which the muscle shows a further peculiarity first noticed by Cunningham (1870), in *Ceryle.* This is a short, strong aponeurosis linking the right and left muscles, near the posterior end of the anterior bellies. This feature was noted in various other kingfishers by Beddard (1896), and has been further checked in a wide range of other species for the present study. The transverse aponeurosis has been found throughout the Cerylinae, but in none of the Alcedininae examined. Within the Daceloninae, it was found in *Tanysiptera, Cittura* and *Halcyon sancta* (=*Sauropatis vagans*) by Beddard, and in the present study also in *Melidora*; it is evidently absent in most, perhaps all, other members of the subfamily.

M. biventer is also well developed in the Indicatoridae and *Jynx.* A weak biventer with short fleshy bellies and a long tendon is seen particularly in the Upupidae, Phoeniculidae, Meropidae, Galbulidae and some Picidae. The anterior belly usually meets or lies close to its contralateral partner in the midline at the insertion, but right and left are separated by a wide gap in the Galbulidae, Meropidae (except *Nyctiornis*) and Picumninae.

M. spinalis cervicis and M. splenius colli (N.A.A.: *M. longus colli dorsalis*)

M. spinalis arises from the neural spines of vertebrae 14 to 18, and inserts by a series of slips on the anapophyses of 2, and of 6 to 13 (5 to 13 in *Malacoptila panamensis*). M. splenius colli has no independent insertion, but consists of a series of slips joining the slip of M. spinalis inserting on 2. There are from three to five of these slips, arising from the lateral surface of the neural spines of successive vertebrae, the most anterior in all cases being 4.

M. splenius capitis

In most species examined, this muscle arises from the neural spine of 2, and inserts on the posterior surface of the skull deep to M. biventer and M. complexus. In *Phoeniculus purpureus* and *Tockus erythrorhynchus* there was additional origin from the neural spine of 3. Right and left muscles generally lie close together in the midline, but a wide gap exists in *Melittophagus pusillus.* The muscle is relatively very large in the Galbulidae.

Cruciform structure of M. splenius capitis, as described by Burton (1971) is clearly evident in *Nonnula ruficapilla*, but barely discernible in most other species examined.

Mm. pygmaei (N.A.A.: *M. longus colli dorsalis, pars profunda*)

Mm. pygmaei are small, weak muscles, originating from the neural arches of vertebrae between 11 and 8, and inserting on the lateral edges of the transverse-oblique crests of vertebrae which are most commonly the second ones anterior to the vertebrae of origin. Asymmetrical distribution of Mm. pygmaei is frequent, and they are completely absent in most of the species examined here. They were found only in some species of Meropidae, Coraciidae, Leptosomatidae, Galbulidae and Bucconidae. Their occurrence in single specimens of various species in these families is as follows:

MEROPIDAE: *Melittophagus pusillus.* Left side, from 8 to 6 and 9 to 7; right side, from 8 to 6, 9 to 7, 10 to 8 and 11 to 9.

Nyctiornis amicta. Absent.

LEPTOSOMATIDAE: *Leptosomus discolor*. Left side, from 9 to 7 and from 10 to 8; right side, from 8 to 6.

CORACIIDAE: *Coracias benghalensis*. On both sides, from 8 to 6, 9 to 7 and 10 to 7.
Eurystomus orientalis. From 9 to 7 on the right; absent on the left.

GALBULIDAE: *Galbula ruficauda*. Left side, from 9 to 6; right side from 9 to 6 and from 8 to 6.
Galbalcyrhynchus leucotis. Present on the left side only, from 9 to 6 and from 8 to 6.

BUCCONIDAE: *Malacoptila panamensis*. From 8 to 6 and from 9 to 7 on both sides. Absent in *Notharcus macrorhynchos, Chelidoptera tenebrosa* and *Nonnula ruficapilla*.

Mm. ascendentes cervicis (N.A.A.: *M. cervicalis ascendens*)
Originating on the diapophyses of all cervical vertebrae except 1 to 5 these muscles each consist of two slips inserting on the anapophyses of the second and third vertebrae anterior to the origin. Thus, the most anterior muscle, originating on 6, inserts on 3 and 4. The series continues posterior to the neck as Mm. ascendentes thoracicis. No noteworthy variation was discovered among the species dissected.

M. longus colli ventralis
This large and complex muscle extends along most of the ventral side of the neck. The main part arises by a series of fleshy slips, starting in the thoracic region, from the sublateral processes, hypapophyses and the anterior region of the centra of successive vertebrae. Insertion is made by long tendons attaching on the cervical ribs; each vertebra sends a slip to join each of the tendons traversing it. In the anterior region of the neck, shorter slips arise from costal processes or sublateral processes, inserting tendinously on ribs or hypapophyses. Some of these anterior slips should perhaps be treated as M. flexor colli profundus; however, their siting and arrangement is so variable among the species studied that it seems impracticable to distinguish this as a separate muscle from M. longus colli.

Complete dissection of M. longus colli to enumerate the siting and arrangement of all slips throughout the study species, would be extremely time consuming. For the purposes of the present study, a more general examination was considered sufficient. The thoracic region was excluded, but particular attention was paid to the short anterior slips. The main features revealed are·as follows: In all species, the most anterior insertion is on the hypapophysis of 2. Insertion on 3 is also on the hypapophysis, but on 4, insertion on the hypapophysis was found only in *Todus, Leptosomus,* and the representative species of Meropidae, Bucconidae. Galbulidae and Picidae; in the remainder, attachment on 4 is to the rib, or costal process. The slips attaching on 2, 3 and 4 are, in most species, short ones, arising typically from the sublateral process of 6, though the slip to 2 arises from the costal process of 5 in *Upupa,* and that to 3 from the sublateral process of 7 in *Phoeniculus.* The main part of the muscle, (consisting of long tendons and their associated fleshy slips) has its most anterior attachment typically on the rib of 5. In the Bucconidae and Galbulidae, long slips attach only as far forward as 6, but extend to 3 in *Upupa* and *Todus*, and to 2 in *Alcedo, Indicator, Jynx* and *Trachyphonus*. In *Momotus,* long slips attach on 2 and 4, but not on 3, while in the Picidae (other than *Jynx*), the entire muscle consists of long and very strongly tendinous slips attaching forward to 2.

M. flexor colli brevis (N.A.A.: *M. flexor colli lateralis*)
The bulk of this muscle originates from the lateral strut of 3 and the lateral processes of 4 and 5; origin on 5 is absent in *Alcedo atthis* and *Malacoptila panamensis*, while in *Campephilus* there is additional origin from the lateral strut of 6. The muscle also includes a smaller, medial portion, originating ventrally (typically on sublateral processes) and separated from the main body of the muscle by anterior slips of M. longus colli. (This portion may well represent a M. flexor colli profundus, merged with M.f.c. brevis; otherwise this muscle is

absent in the species studied). This medial portion appears to be absent in the pecies of Alcedinidae, Upupidae, Phoeniculidae, Bucerotidae, Bucconidae and Galbulide dissected, and in some Picidae (*Sphyrapicus, Sasia*). It is present in the remainder, but varies considerably in development and in its relation to adjacent muscles (especially M. longus colli). In the species examined, it is best developed in *Trachyphonus darnaudii,* in which it actually originates posterior to the lateral portion, on the sublateral process of 6. In other species possessing it, the vertebrae of origin are the same as the lateral part except in *Momotus,* in which the very short medial portion originates from the postlateral process of 3.

Insertion is on the hypapophysis like process on the ventral side of the atlas (processus latus).

M. complexus

The sites of origin of this muscle vary considerably among the families investigated. No single species utilizes all the possible sites of origin, which are the anapophysis of 3; the transverse process and lateral strut of 4, and the diapophyses of 5, 6, 7, 8 and 9.

Insertion of M. complexus is on the dorsal edge of the occipitals, superficial to M. biventer. The muscle is best developed in the Alcedinidae, in which its origins have been checked in a wide range of species. Origin is from 5, 6 and 7 in the Cerylinae and Daceloninae, and from 8 as well in the Alcedininae; attachment to 9 was found in a single specimen of *Alcedo atthis.* Origin of M. complexus posterior to 7 has not previously been reported in any bird.

M. complexus is poorly developed in the Picinae (notably *Campephilus*) and in *Indicator.*

M. rectus capitis superior (N.A.A.: *M. rectus capitis dorsalis*)

This muscle lies superficial and anterior to M. flexor colli brevis, which it much resembles; the two could well be considered as divisions of a single muscle. Origin is from the lateral surface of neural arch 1, from the anterior surface of anapophyses 2 and 3, and in some species from the lateral strut of 4. Insertion is on the posterior edge of the basitemporal plate.

M. rectus capitis lateralis

This muscle inserts on the lateral edge of the exoccipital usually immediately lateral to M. complexus. Origin is commonly from the hypapophyses of 2, 3 and 4, and in *Leptosomus* and *Upupa* from 5 as well. However, the number of sites of origin is reduced in many species; 3 and 4 only are occupied in the Cerylinae and *Coracias,* and 2 and 3 only in the Todidae, Meropidae, *Eurystomus* and *Jacamerops.* Except for *Jacamerops,* reduction is even more marked in the Galbulidae and Bucconidae, with origin only from 3 in the species available for dissection. The muscle shows a corresponding reduction in bulk in these two families, and in *Notharcus macrorhynchos* and *Galbalcyrhynchus leucotis* it can fairly be described as vestigial.

M. rectus capitis ventralis

Origin is from the ventral surface of 1, the hypapophyses of 2, 3, 4 and 5, and commonly also the sublateral process of 6. The latter point of origin is lacking in the Todidae, Momotidae, Meropidae, Phoeniculidae, Bucerotidae, Capitonidae and Ramphastidae. Insertion is on the basitemporal plate, anterior to M. rectus capitis superior. Both this muscle and M.r.c. lateralis are notably bulky in the Picinae, the very deep hypapophyses providing an increased area for their origin.

Mm. intertransversarii and Mm. inclusi

The Mm. intertransversarii connect successive vertebrae, running in most cases between their lateral processes. In the middle of their range, they are of complex, multipinnate structure (see especially Zusi & Storer, 1969). Mm. inclusi are similarly situated, but lie deep to Mm. intertransversarii, and are mostly divided into dorsal and ventral parts (Mm. inclusi superiores and inferiores). They end anteriorly one or two vertebrae before the Mm. intertransversarii. The most anterior M. intertransversarius in Coraciiform and Piciform birds is usually that between 5 and 4; in many species, lateral fibres from 6 also reach vertebra 4. The anterior limit is vertebra 3 in the Capitonidae, Picidae and Coraciidae.

PART 3

Functions and evolution

Bill and skull

The functional significance of bill form in birds is sometimes obvious, but more often rather hard to understand, even when it is distinctive or unusual. Bill modifications in the Coraciiformes and Piciformes are discussed at family level in the Systematic review; problems examined in this section concern more fundamental aspects of jaw action and cranial morphology.

Ideally it should be possible to integrate information on osteology and arthrology with that on muscle action to produce a complete picture of jaw actions and the ways in which they are controlled. In practice, however, this would require a very full understanding of the forces developed by muscles and their sequence of action, and of the physical properties of joints and ligaments. So far, the only analyses of avian jaw action which approach this ideal standard are those made for the Mallard (*Anas platyrhychos*) by Zweers (1974, 1977). Work of this type, involving *in vivo* experimentation and electro-myography was beyond the scope of the present investigation, but the discussion which follows will at least serve to point out problems which would repay more intensive study.

Overall form

Barnikol (1952), following earlier work by von Kripp (1935) distinguished two general types of avian skulls which he called 'streckschädel' (stretched skull) and 'knickschädel' (hooked skull)*. He defined them in terms of two main criteria. In the 'streckschädel' type, the foramen magnum is situated at the back of the skull, and the brain axis makes a relatively small angle with the bill axis; in the 'knickschädel', the foramen magnum is situated more ventrally, and the brain axis makes a larger angle with the bill axes. Barnikol's examples of the former include *Cygnus, Ixobrychus* and *Phalacrocorax;* to them might well have been added various other members of their orders, as well as most of the Gaviiformes, Podicipediformes and some Procellariiformes and Charadriiformes. They are predominantly relatively primitive types specialized for aquatic feeding. The 'knickschädel' is much more widespread; Barnikol selects *Strix, Opisthocomus* and *Scolopax* as examples. He proposed, essentially, that the 'streckschädel' was a relatively archaic skull form which had become exagerrated for functional reasons in certain types, particularly fish eaters. He suggested, furthermore, that positioning of M. adductor mandibulae was an important underlying factor; evolution of the extreme 'streckschädel' allows the external temporal region of the muscle to be sited vertically above its points of attachment on the lower jaw. In the examples he chose, increasingly vertical attachments of M. add.mand.ext. are correlated with an increasingly vertical orientation of the postorbital ligament, which is finally sited slanting backwards to the mandible in *Phalacrocorax.*

The Coraciiformes and Piciformes are more advanced birds than any of Barnikol's 'streckschädel' types and the majority have skulls conforming fairly well to 'knickschädel' morphology. Nevertheless, there are significant variations in the orientation of major skull components, and these deserve to be considered in more detail. Among this assemblage, the Alcedinidae stand out as the clearest example of modification towards 'streckschädel' form, with skulls stretched out along the bill axis, and the palatal apparatus lying almost in the same plane as the tomia of the closed bill. However, difficulties are encountered when Barnikol's criteria are applied. By comparison with, for example, a *Megalaima* barbet, *Ceryle* has M.add.mand.ext. and the postorbital ligament less vertically oriented, while the situation of the foramen magnum scarcely differs. The elongated form of the *Ceryle* skull is, instead more clearly manifested in the low orbit and cranium, and in the arrangement of the kinetic apparatus, with the quadrates sited far back, behind the orbit. In ventral view, the pterygoids of *Ceryle* enclose a considerably smaller angle posteriorly than either *Megalaima* or any other bird included in this study.

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*In discussions throughout this paper I shall use these terms in their German form, to indicate their origin clearly, to avoid possible ambiguities inherent in their English translations, and because they are less clumsy.

It seems significant that the only members of the Coraciiform/Piciform assemblage to clearly show 'streckschädel' features of skull morphology are the one family whose members include fish eaters. Moreover, these features are much more strongly marked in the more thoroughly piscivorous Cerylinae and Alcedininae than in the Daceloninae. The functions and biological roles of 'streckschädel' modifications deserve much more study, but in the present instance, the following suggestions can be made:

(*a*) The combination of low orbits with a palate and bill oriented in a straight line brings the line of vision close to the primary axis of orientation of the bill (see Bock 1964: 28). This is probably of value in minimizing parallax error in a situation which is already complicated by refraction between air and water, and which may require great speed and accuracy in countering evasive action by prey.

(*b*) The skull increases in width from front to back; hence, by siting the quadrates, and thus the mandible articulation as far back as possible, the gap between the posterior ends of the mandibular rami is maximized. This may be an adaptation to swallowing large whole fish, since the rami themselves seem to have only a limited capacity for outward bowing. The long flat palate may also be helpful in this regard, since fish are long food items with less capacity for bending than much of the large prey, e.g. insects, frogs, taken by other Coraciiformes.

(*c*) The gradual, even taper of jaws and skull which is achieved through these modifications may be of some value in streamlining, to permit efficient movement through water.

The posteriorly situated quadrates of *Megalaima* mentioned above, are a rather unusual feature among the Coraciiform/Piciform assemblage, though characteristic of many Capitonidae and the Ramphastidae as well as Kingfishers. As in the Alcedinidae, this may well be an adaptation for swallowing large food items, in this case fruits, by increasing the gap between the mandibular rami. The accompanying feature of palatines, pterygoids and jugals lying more or less in the same plane as the tomia of the closed bill is more widespread, though only in the Alcedinidae does this involve the 'streckschädel' feature of a reduced angle between the pterygoids. It is seen particularly among the Coraciiformes, other than the Upupidae, Phoeniculidae and Bucerotidae, and in the Galbuloidea. In the Todidae, Galbulidae and still more the Meropidae, this is combined with a high cranium and very ventrally situated foramen magnum to produce skulls with an extraordinary profile, the front of the skull sloping down sharply to a low and rather flattened upper jaw base. This shape, and the position of the foramen magnum, is perhaps related to perching posture, in which the bill is normally tilted up at a considerable angle as the bird scans the sky for prey.

Viewed dorsally, considerable variation is seen in the extent to which the skull narrows from posterior to anterior. Narrowing in front of the orbits must be connected largely with the extent of forward vision. The most pronounced narrowing by far is seen in the Phoeniculidae, and is probably connected with feeding by gaping. Lorenz (1949) pointed out that passerine 'gapers' in the families Sturnidae and Icteridae look forward between the mandibles as they part them when feeding, and Beecher (1953*a*) showed that their ectethmoids are notched to increase their capacity for forward vision. It is puzzling that the Upupidae do not also have the skull narrowed in front of the orbits, since they feed in a similar manner, but on the ground. Perhaps the substrates in which they gape impose forces necessitating a more broadly based upper jaw.

The skull is also quite markedly narrowed in front of the orbits in the Indicatoridae, *Jynx* and many woodpeckers, again probably enabling them to look forward at prey or a substrate at close range. Moderate narrowing from posterior to anterior is seen in the Meropidae and Galbulidae, but in this case probably reflects more the distinct broadening of the posterior cranium in these families, a feature believed to be related to neck muscle action (q.v.). Most other families examined have skulls which are relatively very broad anterior to the orbits, and this is in most cases undoubtedly related to the need for a large gape. In the case of the Alcedinidae this creates a problem, since as explained earlier, one function of their 'streckschädel' skulls seems to be to bring the line of vision as close as possible to the primary axis of orientation of the bill; the advantage of this adaptation would seem somewhat offset by the resulting reduction of forward vision. A partial compensation may be provided by the emarginated shape of the lacrimal.

Kinesis

The mechanics and functional significance of cranial kinesis in birds have been discussed at length by Bock (1964), who distinguishes two principal mechanisms. In *uncoupled kinesis,* the movements of the jaws are entirely independent; in *coupled kinesis*, depression of the lower jaw cannot take place without simultaneous raising of the upper. The principal structure on which coupled kinesis depends is the postorbital ligament, which is present in the majority of birds. An alternative way of achieving coupling is by means of an interlocking device at the quadrate/mandible hinge. This arrangement is uncommon, occurring sporadically amongst several unrelated groups of birds; these are listed by Bock (1964), and to this list must now be added *Bucorvus* and *Megalaima* (see p. 29–30).

Even where a postorbital ligament is present, uncoupled kinesis is possible when the ligament is unloaded (slack), a condition which occurs when M. protractor is contracting ahead of M. depressor. The mechanisms involved, and the variety of possibilities between strict coupling and total independence, are discussed by Zusi (1967), while Zweers (1974) provides detailed analysis of a closely coupled system in the Mallard. Some independent jaw action is even possible in forms with articulation lock coupling, such as *Bucorvus* and *Megalaima,* through spreading of the lower jaw rami. A critical point concerns the extent of retraction possible for the upper jaw in birds with coupled kinesis. Bock suggested that retraction past the normal closed position was impossible for birds possessing a functional postorbital ligament, but Zusi (1967) musters observational evidence to the contrary. Certainly at least some Coraciiformes and Piciformes are capable of this feat (see below). Presumably there is some relation between the extent of development of a postorbital ligament or articulation lock, and the extent and frequency of independent jaw action, but the relation is not a simple one, as indicated by the distribution of these features in families considered here. However, the possible biological roles of these mechanisms among Coraciiform and Piciform birds will be briefly reviewed as far as possible.

(*a*) COUPLED KINESIS. A closely coupled system appears particularly suitable where rapid jaw action is needed (Bock, 1964), and would seem particularly important for those species, mainly Coraciiform, which capture agile or aerial prey. The required acceleration must be achieved with minimum sacrifice of power, since the prey may need to be gripped strongly once captured—unless the initial snap of the jaws has sufficed to kill it, as must often be the case with small insects. Kinetic coupling may also be of special importance where forceful protraction of the upper jaw is required, in species which forage by 'gaping', i.e., inserting the jaws into the substrate and then opening them. Coupling in this situation enables the force of M. depressor mandibulae to be added to that of M. protractor (see discussions by Zusi, 1959, 1967; Manger Cats-Kuenen, 1961; Bock, 1964); this is of greatest importance in the Upupidae, Phoeniculidae and some Bucerotidae. *Bucorvus,* which possesses a well developed articulation-lock device obtains most of its food on the surface, but probably requires closely coupled jaw action for swift prey seizure. The significance of the weak articulation lock in *Megalaima* spp. is more puzzling, especially as they may have a significant need for independent jaw action in some circumstances (see below).

An aspect of coupled kinesis which has not received enough attention is the role of the musculature in guidance. This emerges very clearly from the work of Zweers (1974) on the Mallard, *Anas platyrhynchos.* The very strongly coupled kinetic system of this bird depends for its effectiveness on the action of the internal adductors in guiding the movements of quadrate, pterygoids and palatines. Exactly how the guiding and power roles of the jaw musculature would be fulfilled among the varied members of the assemblage studied here can scarcely be surmized at present. An understanding of this point would require much more precise information of their jaw movements than is at present available—a level of study possible only under controlled conditions in the laboratory.

(*b*) Uncoupled kinesis. The independent jaw action made possible by uncoupled kinesis is important where skilful manipulation of food is at a premium, since upper and lower jaws are thus enabled to vary the angle and position in which they meet one another. A particularly valuable faculty in some birds is that of depressing the upper jaw past the normal closed position, with the lower jaw itself still partly depressed. The jaws can then be brought parallel, or even opposed with their tips closer together than the basal region. In bird photographs, evidence of retraction past the normal closed position is occasionally seen, when the tip of the lower jaw appears to extend beyond that of the upper, despite clearly undamaged bill tips.

Uncoupled kinesis is likely to be most needed when dealing with slippery or awkwardly shaped prey, or when several objects need to be gripped along the length of the bill. Thus, the weak development of the postorbital ligament in the Alcedininae and Cerylinae may be related to the need for skilful manipulation when dealing with fish. Retraction past the closed position is of limited extent in kingfishers, due to an effective retraction stop (see below), but apparently does occur; in a photograph of *Alcedo atthis* by Massny (1977) the lower jaw tip extends appreciably further forward than the upper. Among the Piciformes, similar problems may arise in dealing with large numbers of prey. Photographs of *Jynx* with a mass of ants held in the bill (Koffán, 1960) demonstrate independent jaw action excellently. The photograph shows the upper jaw tip retracted far behind the lower in a most convincing way. Note that the diagram of *Sphyrapicus* with the lower jaw projecting while closed in Spring (1965) must be of the bird with a damaged bill which the author refers to on p. 486; the position shown could not be attained by any normal jaw action. Barbets holding several fruits at once in the bill seem to face a similar problem (photograph in Thomson, 1964), but although most lack a postorbital ligament, they are not able to retract past the closed position, as further retraction is halted by a bony stop (see below). It is puzzling, though, that some Capitonidae have evolved a degree of articulation coupling, which has the same effect as a postorbital ligament, and for that matter, that the Ramphastidae have not.

Safety devices

During the processes of feeding and nest excavation, the skull is subjected to a variety of forces which have a profound influence on its morphology. Under the general heading of safety devices are included various osteological or arthrological features which serve to confine jaw and palate movements within safe limits, or otherwise to withstand potentially hazardous forces. Constraints, on movement are basically of two kinds; 'stops' are devices which limit the range of normal movement, especially that of kinesis, while guides and braces control direction and prevent abnormal movement caused by interaction with prey or objects in the environment. Stops are to be regarded as the final, ultimate limit on movement; in practice, the muscles and ligaments involved will normally arrest a movement before these extremes are reached. A review of kinetic stops, principally in waterfowl, is given by Fisher (1955).

As will be seen below, special modifications are present in woodpeckers to sustain forces incurred during excavation for food. It is interesting to note in passing that many other members of the Coraciiformes and Piciformes excavate wood or other hard substrates to create nest sites, yet lack special adaptations for doing so; even the frail skulls of the Todidae can cope with burrowing (Kepler, 1977). Presumably this is because nest excavation can be spread over a long enough time to allow even rather feeble excavating actions to suffice. Thus, the requirements of feeding remain the overriding force determining the architecture of skull and jaws.

Protraction stops

A potential stop on protraction in nearly all species is provided by the orbital process of the quadrate; when this touches the wall of the orbit, all forward movement of the palate must inevitably cease. How significant this is in practice is hard to judge. Some birds, such as typical Larids (Zusi, 1962), *Corvus* (Fisher, 1955) and some hornbills (present study) have a swelling on the orbital wall which would make early contact with the orbital process. In other birds, (notably the Alcedinidae in the present study), the position of the orbital process, far from the orbital wall, would render it quite useless as a stop. In between are a large number of birds in which the orbital process could possibly act in this way, but which lack special modifications. It is quite certain, however, that the orbital process cannot act as a stop in species which have M. protractor quadrati (q.v.) attached along its full length.

In this connection it is interesting to compare the Upupidae and Phoeniculidae with the Picidae (except *Jynx*). All three families have M. protractor greatly enlarged, and would seem to run an appreciable risk of dangerous over-protraction in the course of foraging. In the Upupidae and Phoeniculidae, the orbital process is free; it could well serve as a protraction stop, particularly in *Rhinopomastus.* These two families show no other obvious limitation on protraction, and it is possible that during the relatively slow action of 'gaping' there is little danger of sudden uncontrolled increases in this force.

By contrast, in the Picidae, M. protractor quadrati has attachment along the full length of the orbital process, and although it lies close to the orbital wall, it hardly seems possible for the two to touch, and thus stop protraction. Nevertheless, woodpeckers are at considerable risk. Hammering is assumed (Spring, 1965) normally to generate retraction forces on the bill, opposed by M. protractor, but a slight error, or unexpected irregularity in the wood might well add suddenly to protraction, instead of counteracting it. To safeguard against such eventualities, woodpeckers have an alternative stop mechanism in the form of a fronto-nasal hinge in which the frontal bulges out to overlap the upper jaw. This is not equally developed in all woodpeckers; Burt (1930) has demonstrated in a range of species that increasing development of this feature is correlated with increased size of M. protractor, decreased kinesis and greater dependence on hammering as a foraging method. Zusi (1962) has proposed a rather similar stop mechanism in *Rhynchops,* and the form of the fronto-nasal hinge suggests the same principle in various Strigidae and a few Falconidae. [The greatly developed casque of many Bucerotidae provides an alternative stop mechanism in the region of the fronto-nasal hinge, though this may not be its primary function; see Manger Cats-Kuenen, 1961].

Retraction stops

The fundamental stop on retraction occurs when upper and lower jaws meet; in addition, for most birds studied here, contact between the nasal bar and the dorsal anterior rim of the orbit (formed by lacrimal, ectethmoid or frontal) provides a further stop. This latter stop is discussed at length by Cracraft (1968), who points out that no locking mechanism exists which would eliminate muscular effort in retraction—a function of stops which had been proposed by Fisher (1955). In any case it is doubtful if such a device would provide any significant advantage, for reasons discussed elsewhere (Burton, 1978). The lacrimal-ectethmoid complex provides the firmest stop when a large ectethmoid forms or supports the stop. This condition is best realized here in the Upupidae, Phoeniculidae, Bucerotidae and Piciformes (other than Galbulidae and Bucconidae). The lacrimal forms the stop in the remainder except for the Momotidae which lack it, and rely on the frontal; even where it is much enlarged, as in the Alcedinidae and Coraciidae, it probably always produces a more resilient stop than the ectethmoid. In the Picidae, an additional stop is provided for many species by the very long anterior process of the opisthotic, which meets and articulates with the quadrate.

Cracraft questions why retraction stops are necessary at all, since the lower jaw would appear sufficient. He suggests that external forces encountered during feeding may produce unusual movements which require this safeguard. Among the families considered here, large ectethmoids and firm retraction stops occur mainly in birds which excavate for their food (gapers and hammerers) and in fruit eaters; the latter may perhaps incur hazardous external forces during the wrenching movements sometimes needed to detach fruits from trees. Another situation in which retraction stops may be needed, not considered by Cracraft, would occur in uncoupled kinesis if the upper jaw is retracted past the normal closed position while the mandible remains partly depressed. In the Alcedinidae, this apparently occurs to a moderate extent, and the stop, formed by a large lacrimal, is indeed effective in bringing further retraction to a halt. It is interesting to note, though, that in a specimen of *Ceryle alcyon* with missing lacrimals, retraction much more extensive than could conceivably occur in life was possible without damage. Still more surprising, in *Jynx,* which regularly uses extensive retraction past the closed position, there is apparently no functional stop other than the limit imposed by the structure of the articulation of the quadrate and cranium. The fronto-nasal hinge here is simply flexible enough to sustain extensive retraction. Experiments with a freshly dead bird indicate a figure of approx. 20°–25° for the maximum retraction obtainable by muscle action, but by manipulation this could be extended to 55° without damage. Barbets and toucans mostly lack a postorbital ligament, and presumably have uncoupled kinesis, at least where there is no articulation coupling. Despite this, they apparently lack the capacity for retraction past the closed position, with retraction halting totally when the posterior medial surface of the ventral bar contacts the frontal, supported by a substantial ectethmoid.

Support of the jugal bar and palatines

Cracraft (1968) has described various modifications of the lacrimal-ectethmoid complex which appear to have the function of bracing the jugal bar against dorsally, and in some cases medially directed forces. He quotes Bock's (1960*a*) suggestion that the brace may prevent disruption of the jugal when food is being crushed, but notes 'of interest, however, is the fact that many species, which are close relatives of birds with a brace, lack the brace, but yet probably would derive advantage from possessing one'. This problem still remains unresolved, and this review only serves to re-emphasize it. Most Coraciiformes and Piciformes possess some sort of jugal brace, with the exception of the Momotidae, Capitonidae and, perhaps, Ramphastidae. In the latter family, the ventro-lateral corner of the ectethmoid is produced into a process which makes contact with the jugal bar where it broadens to join the maxillo-palatine—a position which scarcely seems to require bracing. Nor does this process seem to act as a retraction stop, for when skulls are manipulated, retraction is halted by the frontals before the maxillo-palatine makes effective contact with it. The slip of M. pterygoideus attached on the maxillo-palatine passes under the ectethmoid just medial to this process, but would be well flattened during strong retraction. The Capitonidae and Ramphastidae eat a large proportion of fruit, and apparently swallow much of it whole; possibly for these birds, the danger of disruption when crushing food is fairly small. The case of the Momotidae is much more puzzling, as much of their animal food surely requires fairly powerful crushing. Perhaps there is some positive selective advantage for losing the brace in this case, but it is difficult to see what this might be.

Bracing of the palatines by a wide ectethmoid is seen in a number of bird families feeding on aerial insects, e.g. Caprimulgidae, Apodidae, Hirundinidae. Cracraft suggests that it may serve to protect the palatines against impacts with moving prey. The Coraciiformes and Piciformes, although including various aerial insect feeding groups, show few clear examples of such a brace. The two principal families which feed in this way, the Meropidae and Galbulidae, catch their prey with the tip of a long bill, and forces on their palatines are unlikely to be abnormal. The Meropidae totally lack any indication of such a brace, while in the Galbulidae, *Galbula* has a wide ectethmoid lying near the palatine (though part of M. pterygoideus dorsalis intervenes between the two) but this is much reduced in *Galbalcyrhynchus.* A possible ectethmoid brace exists, however, in *Indicator* and *Jynx,* though its function is unclear; perhaps it is connected in the latter with the large mouthfuls of insect prey which are collected to feed nestlings. In the Coraciidae, the anterior ventral edge of the inflated lacrimal lies close to the palatine. In *Coracias* and the Brachypteraciinae, it is so far forward that it probably adds little to the support already available from the fused maxillo-palatines (see below). In *Eurystomus,* it lies somewhat further back, and may be of some value to this specialized aerial feeding genus, with its strongly widened palatines. *Chelidoptera* feeds in a similar way, but its ectethmoids are situated too far above the palatines to have any value as a brace.

Desmognathy

Much attention was given during the nineteenth century to the variations of palatal structure first described in detail by Huxley (1867). Attempts to interpret these at the time followed mainly phylogenetic reasoning, and surprisingly little attention has been paid to them since, despite the greater concern given to functional anatomy by more recent workers. Among the Coraciiformes and Piciformes the presence or absence of the desmognathous condition (in which the maxillo-palatines are fused in the midline) is a feature of considerable interest. It would appear that this condition is derived from a schizognathous or aegithothognathous one rather than the reverse; various intermediate stages can be seen in the Capitonidae.

This condition is found throughout the Coraciiformes, but within the Piciformes it is seen only in the Galbuloidea, the Ramphastidae, and, weakly developed, in some Capitonidae. The Ramphastidae, like the Bucerotidae, have the anterior part of the palatines fused as well, producing the condition which Beddard (1898) termed 'doubly desmognathous'. This is presumably in some way a consequence of the evolution of massive bills in these two families, though whether through mechanical necessity or for ontogenetic reasons is uncertain.

The desmognathous forms include a large proportion of birds which feed on active, and often large animal prey, and it is possible that desmognathy provides some support against stresses incurred through killing and consuming such prey. Significant forces would be those acting across the bill axis; those acting along it are more a feature of birds which excavate for food, and resistance to them would scarcely be improved by midline fusion of the maxillo-palatines. Those acting across the bill include upward forces, produced by gripping or crushing prey, and lateral ones, either directly across or twisting (i.e. with a dorsal or longitudinal component). Simple upward forces would meet some resistance from well developed maxillo-palatines, but these need not necessarily be joined; the crucial feature of fusion seems most relevant where lateral forces are involved. An important factor here may be the technique of beating prey against the perch, used by many species to kill or immobilize their victims. This is commonly performed sideways, and though the prey is the primary target, the bill often makes contact with the perch as well. The forces involved are necessarily large, since feeble blows would fail in their purpose. It is perhaps significant that passerines lack midline fusion of the maxillo-palatines, their expanded vomers supporting them only against moderate dorsally directed forces. Although some passerines, such as crows and shrikes, regularly take large and vigorous prey, their methods of subduing it do not include the highly developed beating behaviour of the Coraciiformes and Galbuloidea.

Desmognathy has also some relevance to the evolution of an M. pterygoideus dorsalis with attachment on the maxillo-palatine, as seen in several Coraciiform and Piciform groups. Such an attachment requires at least a strong maxillo-palatine; since unilateral action could impose severe stress on the maxillo-palatine, desmognathy would seem to be almost essential as well. In fact, the majority of species in which M. pterygoideus is attached on the maxillo-palatine are desmognathous. Exceptions occur only among the Capitonidae, in which slight muscle attachment on the maxillo-palatine is present in some species which are scarcely or not all desmognathous; any increase in such attachment, however, might be expected to be closely accompanied by increased desmognathism. This may have been a key factor in the evolution of the Ramphastidae from barbet ancestors (see Systematic Review, pp. 433–434).

Pterygo-palatine articulation

The Indicatoridae and the Picidae (including *Jynx*) differ from all other families studied here in the form of the pterygo-palatine articulation, with a long pterygoid foot overlapping the palatine dorsally and medially. This arrangement would seem less prone to disarticulation than the short articulation of other families, but it is far from clear why it has only arisen in these two groups. The change may have involved transfer of the epipterygoid from the palatine (with which it normally fuses) to the pterygoid, but no nestlings were available young enough to compare its ontogeny between these two families and others.

Lower jaw

The movements of the lower jaw are generally simpler than those of the upper, except insofar as the two are correlated by kinetic coupling. An exception to this is seen in birds which possess the capacity to widen the gap between the mandibular rami by the action of M. pterygoideus ventralis medialis; the pull of this muscle on the internal process of the mandible rotates it on the quadrate articulation, bowing the rami outwards. Though this mechanism has been described from various unrelated taxa, such as the Procellariiformes and Charadriiformes (Yudin, 1961), Columbiformes (Burton, 1974*b*), Caprimulgiformes (Bühler, 1970, 1980) and probably *Pelecanus* (Burton, 1977*b*), it appears to be absent, or scarcely developed in most Coraciiformes and Piciformes. Flexible zones within the mandibular rami are obviously a prerequisite, but are virtually lacking in the majority of species examined. A small degree of flexibility which would permit moderate bowing seemed to be present in skulls of *Alcedo, Leptosomus* and *Jynx,* and with fresh material might be demonstrated in a few more. Nevertheless, this faculty seems to be of little significance in the feeding methods of the Coraciiform-Piciform assemblage. This is somewhat surprising in view of the many members of this assemblage which swallow large prey whole. Presumably flexible rami would be incompatible with other mechanical demands, such as those of prey beating. It should also be noted that Coraciiform and Piciform birds do not feed their young by regurgitation, a process which involves mandible bowing in some groups of birds.

For the majority of birds, there is relatively little danger of excessive depression of the lower jaw—an event only likely to be brought about by unusual environmental forces, such as those encountered by *Rynchops nigra* (Zusi, 1962). Consequently, there is no system of bony stops, the main limitation on movement being the post orbital ligament, acting in conjunction with the upper jaw apparatus. However, the lower jaw is exposed to other hazardous forces, for which various support mechanisms exist, as follows:

(*a*) *The internal and external jugomandibular ligaments.* The internal ligament resists backward disarticulation; the external resists downward and perhaps forwardly directed forces. Both are present throughout the families studied except the Picidae. Their lack of the external jugomandibular ligament is presumably directly related to the development of the opisthotic ligament which partly takes over its function.

(*b*) *The occipito-mandibular ligament.* Universally present (though very weak in *Jynx*), and very strongly developed in the Upupidae, Phoeniculidae and Bucerotidae. In at least the first two of this group of families, the large size of the ligament is likely to be related to feeding by gaping and probing. The occipito-mandibular ligament resists forward disarticulation of the mandible, and forces tending to cause this are most likely to reach significant levels when the bill is being extracted from some substrate (see Burton, 1974*a* for discussion of this situation as it affects probing shorebirds).

(*c*) *The quadrate condyles.* The primary role of the condyles is, of course, in articulation of the mandible in normal movement. However, the form of the medial condyle in some families studied here suggests a possible additional function in resisting disarticulation. This is most clearly seen in the Bucconidae, in which the medial condyle projects ventrally well beyond both the other condyles and the pterygoid articulation. It is flattened in the same plane as the pterygoid, and oriented to project slightly forwards and outwards; the tip is swollen and rounded. Less extreme versions are seen in the Galbulidae, Coraciidae and Leptosomatidae and to some extent even in the Momotidae and Meropidae.

Experimentation with prepared skulls quickly shows that this deep medial condyle would be ineffective in resisting anteriorly or posteriorly directed forces, but firmly resists a force acting medially. Forces acting across the jaw in this way may well arise during prey beating, a technique regularly employed by these families, or when swallowing large prey. Kingfishers lack a deepened medial condyle however, despite the fact that they beat fish vigorously, and consume quite large ones whole.

It should be emphasized that a medial condyle of this form must inevitably have other functions as well. It must play an important part in coupled kinesis, although it is unable to bring about coupling in itself, like the specialized medial condyle of *Bucorvus* and some barbets. Its shape is highly efficient for spreading the mandibular rami during jaw closure, though admittedly this also happens perfectly well in birds with an unspecialized medial condyle. Its depth, in the Bucconidae especially, brings the centre of rotation of the lower jaw unusually far below the cranium; the significance of this is unknown. It certainly merits much further study, for it may be an important feature in the evolution of the Galbuloidea and Coraciiformes (see Systematic Review, p. 430).

(*d*) *The medial brace.* This feature was first described in *Rynchops nigra* by Shufeldt (1890) and subsequently in a wide range of birds by Bock (1960*a*). Its functions in *Rynchops* were further studied by Zusi (1962).

As Bock points out, all structural features of the brace suggest that it serves to prevent disarticulation of the mandible when the bill is opened. He further proposes that it compensates for inadequate protection by the quadrate condyles when the jaw is widely opened. The distribution of the brace among the families examined here supports these proposals. The brace occurs only in families which regularly feed on large or active prey, and often need to open the jaws widely; it is absent in groups which are primarily fruit eaters and in those which probe or excavate for insect prey. Three families appear to form an exception; these are the Leptosomatidae, Galbulidae and Bucconidae, all of which lack a medial brace. However, these are also families possessing a very deep medial quadrate condyle. This provides a high degree of protection for the articulation, even with jaws open (see above), and also has the effect of holding the lower jaw so far from the basitemporal region of the cranium that secondary articulation is impossible.

On the basis of this reasoning, a deep medial condyle or a medial brace might seem to be alternative derived mechanisms fulfilling the same function. They are not necessarily mutually exclusive, however. The Coraciidae, for example, seem clearly to have a common origin with the Leptosomatidae, and still possess a fairly deep medial condyle (rather reduced in *Eurystomus*), but have a medial brace as well. Perhaps during the evolution of the Coraciidae, the medial condyle has been reduced due to some other factor(s) to the point at which a basitemporal articulation—and thence, a medial brace—could develop. The medial brace thus needs to be treated with some caution if used as a taxonomic character.

Jaw muscles

M. adductor mandibulae externus

M. add. mand. ext. raises the mandible; it also retracts the mandible against the quadrate, rocking it backwards about its articulation with the cranium, and thus aiding retraction of the palate and depression of the upper jaw. (M.a.m.e. caud, arising on the quadrate, is unable to affect the upper jaw in this way). It is generally the most complex of the jaw muscles, and its structure varies greatly among the Coraciiformes and Piciformes. Fortunately, sufficient information is now available from other orders to give at least an outline picture of its evolutionary history. This wider perspective is essential, for the structural diversity of the muscle cannot be adequately interpreted in purely functional terms.

Among species studied here, the most complex M. add. mand. ext. is seen among the Phoeniculidae. In this family, the muscle includes several well defined components which are absent from the great majority of birds of other orders so far studied. An important exception is provided by the Anatidae; many members of this family possess a complex M.

add. mand. ext. which is remarkably similar in its components and arrangement to that of *Phoeniculus* and *Rhinopomastus*. An approach to this condition is also shown by some Charadriiformes, e.g. *Chionis* (Burton, 1974*a*). In the comparative discussion which follows, reference should be made to Table I for clarification of the terminology used for this muscle by previous workers; a fuller account of synonymy for M. add. mand. ext. is given by Starck & Barnikol (1954).

The complex condition of M. add. mand. ext. seen in the Phoeniculidae and Anatidae is characterized by two main features:

1. The presence of a postorbital lobe, i.e. a section originating directly from the postorbital process, dorsal to M.a.m.e. rost. temp. This is represented in some families (e.g. Alcedinidae, Upupidae) by a single slip, but in its fully developed form (e.g. Phoeniculidae, Anatidae), there are two parts. The dorsal part arises fleshily from the postorbital process, and is attached to the mandible via an aponeurosis, while the more ventral and medial one arises by an aponeurosis from the postorbital process, and its fibres fan out across the lateral surface of the mandible.

2. A relatively narrow insertion of M.a.m.e. vent. The fan shaped sheet of fibres arising from Ap. 2 which constitutes this division of the muscle in most birds is replaced by similar sheets also inserting on the lateral surface of the mandible, but arising from either the postorbital lobe (ventral part), or from an expanded M.a.m.e. caudalis, or even from M. adductor posterior. This arrangement, but without a postorbital lobe, is also seen in Picidae (other than *Jynx*).

Regarding the first of these features, although the evolutionary history of the postorbital lobe has been little discussed by previous workers, its presence in the Anatidae at least is well documented. It was noted by Lakjer (1926) in *Oedemia* (=*Melanitta*) *nigra*, and included in his terminology for M. adductor mandibulae externus superficialis, which is approximately equivalent to M.a.m.e. rostralis as understood here. The same terminology was followed by Goodman and Fisher (1962) in their study of waterfowl. A complication found in the Anatidae (but not the Phoeniculidae) arises from the coalescence of the postorbital and zygomatic processes. This has merged M.a.m.e vent. with M.a.m.e rost. Starck and Barnikol (1954, Fig. 11) regard M.a.m.e. vent. (=Ap. 2 portion) in *Anas platyrhynchos* as the lower half of a bipinnate muscle whose dorsal part is M.a.m.e. rost. temp. (=Ap. 1 portion, ex. temp.). Lakjer (1926) and Goodman and Fisher (1962) treat the whole unit as M.a.m.e. superf., 1a portion ('levator anguli oris'). If Starck and Barnikol are correct, which I believe to be the case, then M. add. mand. ext. medialis (MII) of Lakjer and of Starck and Barnikol is not equivalent to M.a.m.e. vent.—as, on terminological grounds it should be—but, roughly, to M.a.m.e. rost. med.

Turning to the second feature noted above, particular interest centres on the contributions of M.a.m.e. caudalis and M. adductor posterior to the more ventral and posterior sheet of muscle on the lateral surface of the mandible. In the Phoeniculidae, (as in the Picidae, discussed later) this is provided entirely by fibres from M.a.m.e. caudalis. Interestingly, this is also the case in *Chionis* (Charadrii), leading Yudin (1965, fig. 71) to label it incorrectly as M. add. mand. medialis (=M.a.m.e. vent.). (See Burton, 1974: 122).

Among the superficially similar Anatidae, however, the situation is more complicated. Here, M.a.m.e. caudalis itself is not widely expanded, but is closely associated, or even fused with an extensive lateral insertion of M. add. post. This has led to some confusion. Lakjer (1926) figured *Oedemia* (=*Melanitta*) *nigra*, which happens to be a species in which M.a.m.e. caudalis is somewhat reduced, and completely overlaid anteriorly by M. add. post.; his figures 121 and 122 depict this correctly, a point I have checked by dissection. Goodman and Fisher (1962) who follow Lakjer's terminology, also label the fibres on the ventral lateral surface of the mandible as M. add. post. in other waterfowl, though in the two of their figured species which I have dissected (*Spatula clypeata, Mergus merganser*) the posterior edge of this group of fibres is contributed by M.a.m.e. caud. (But note that Goodman and Fisher's 'a' and 'b' parts of M. add. post. do represent a real division of this muscle in *M. merganser*). Starck and Barnikol (1954) go to the opposite extreme by labelling the equivalent region in *Anas platyrhynchos* as 'Ap. 3 post.' (=M.a.m.e. caud.). In this species (and *S. clypeata*) M. add. post. and M.a.m.e. caud. are thoroughly fused, but most of the lateral fibres come from M. add. post., as in other ducks. In a goose, however, (*Anser anser*, fig. 29), Starck and Barnikol label the lateral ventral fibre sheet as M. add. post. Clearly there is scope for much further investigation of the relative development of these two muscles, and not only in waterfowl.

Although the similarity between M. add. mand. ext. in the Phoeniculidae and Anatidae does not extend to all points of detailed structure, there are still enough features in common to require explanation, the more so since clear echoes of the same condition are seen in some Charadriiformes. These three groups can scarcely be considered as close relatives, and it is difficult to envisage convergence as a factor in such totally different birds. More probably, the complex state of M. add. mand. ext. in the three groups should be regarded as a primitive feature, and similarly any traces of it which remain in other families, e.g. the postorbital slip in kingfishers, or the narrow M.a.m.e. vent. and extensive M.a.m.e caud. in the Picidae. Probably future studies will reveal similar conditions in other groups, and perhaps shed further light on the evolution of components of M. add. mand. ext.

As a corollary of this view, the simpler structure seen in most birds is a derived one; this is characterized by a narrowly inserting M.a.m.e. rost. lacking any postorbital lobe, and M.a.m.e vent. which alone forms the sheet of fibres inserting on the lateral surface of the mandible, and a short M.a.m.e. caud., situated deep and partly concealed by M.a.m.e vent. This general derived condition is widespread, and has clearly arisen more than once, and probably many times. It can therefore scarcely be regarded as a useful taxonomic character in itself, any more than can the presumed primitive state. Nevertheless, detailed comparison reveals differences between groups which are consistent enough to be significant, such as those between the Coraciiformes and Piciformes. Such consistent differences may indicate that the simplified condition was derived independently in the two groups.

It may be noted that the Phoeniculidae still retain the primitive condition, and thus the Upupidae and Bucerotidae which seem closely related to them (see p. 426–429) probably represent two more independent lines in which a simplified condition has been attained among the Coraciiform/Piciform assemblage.

It is interesting to observe that here again, as in many other respects, the Galbulidae and Bucconidae resemble the Coraciiformes rather than the Piciformes. The position within the Picidae is also somewhat unclear; the derived condition is only fully developed in *Jynx*, which resembles barbets, toucans and honeyguides in its wide, flattened M.a.m.e. rost. lat., and in the form of M.a.m.e. vent. The implications of this are discussed further in the systematic review (p. 434).

So far, there has been little consideration of functional aspects. In the foregoing discussion, an underlying assumption has been that the components of M. add. mand. ext. function simply to contribute to the forces of adduction and retraction, rather than possessing distinctive additional functions of their own. This is, no doubt, an oversimplification, but one that probably comes fairly close to the truth, leaving unaffected the general evolutionary picture which has thus far been depicted. Any distinct local functions of components of M. add. mand. ext. would probably concern stresses on the mandibular ramus; thus, for example, the balance between the forces of M. add. mand. ext. on the lateral surface of the mandible and M. pseud. prof. on the medial surface must in some degree influence the structure of both muscles. However, adduction and retraction remain overriding factors, the contribution of components varying with their situation. The more dorsal parts of the muscle have a greater moment arm, and consequently provide more force in adduction; they also act over the greatest distance, and generally show fairly simple fibre arrangements. In passing, it may be noted that the most dorsal component of all (in the absence of a postorbital lobe), M.a.m.e. rost. temp., normally has strongly bipinnate structure. This is the inevitable result of the way in which its fibres are attached, around the edges of the temporal fossa. A parallel fibred structure would waste much of the potential surface for origin. Ventral parts, particularly M.a.m.e. caud. have a shorter moment arm, and also act over a shorter distance; in consequence, strongly multipinnate fibre arrangements are characteristic of this section of the muscle (see Gans & Bock, 1965).

Although components within a complex M. add. mand. ext. like that of *Phoeniculus* may have only limited significance individually, the overall result is a bulky and presumably strong muscle, with extensive aponeurotic surfaces for fibre attachment. Birds which have attained a simpler structure in this muscle have lost some potential sites for origin or insertion of fibres, and may, when required, create new ones by branching of existing aponeuroses. This is well illustrated within the passerines (e.g. Bock, 1960*b*) or among waders (Burton, 1974*a*). In such cases of secondary structural complexity, a region of the muscle which is often elaborated is M.a.m.e. rost. med.—as, for example, the 'Ap.D. slip' of the Scolopacinae described by Burton, 1974*a*. Within the Coraciiformes and Piciformes, M.a.m.e. rost. med. is relatively poorly developed; perhaps because M.a.m.e. rost. temp. has remained well developed in many members of the two orders.

The exact extent of M.a.m.e. rost.temp. does, nevertheless, vary a good deal among the birds studied here, and, as in many groups, there appears to be a distinct correlation with body size. (And also with reduction of the lateral portion of M. pseudotemporalis superficialis). A very limited temporal origin is characteristic of small species, and is often associated with overall simplicity of muscle structure, and reduction in pinnate fibre arrangements. This is, no doubt, simply one of the many consequences of the relation between body size (weight varying as the cube of linear dimensions) and strength of components (proportional to cross sectional area, and hence their square). It is tempting to speculate, however, that fluctuations in size within the line ancestral to a species may have influenced its present structure. To take M. add. mand. ext. as an example, structural simplification may in many cases have arisen within small species; components which disappeared in such species could have thus been lost forever, even if their descendants subsequently evolved larger body size.

M. pseudotemporalis superficialis

Among the families considered here, this muscle ranges from a bulky structure of complex architecture to a slip which is vestigial or even absent. A crucial point in understanding this variation appears to be the relative development of lateral and medial regions of the muscle. A highly developed lateral lobe can with confidence be regarded as a primitive feature of the muscle, being exhibited by several unrelated non-passerine groups. In some of these—e.g. among the Laridae—it extends substantially onto the temporal surface of the skull, deep and somewhat dorsal to M.a.m.e.rost.temp. Reduction of this lateral portion appears to be an evolutionary trend common to many avian groups, and generally strongly correlated with reduction of M.a.m.e.rost.temp. In the groups surveyed, a lateral portion is best developed in some families of Coraciiformes, and within this order there is little development of a medial region, even where the lateral origin is much reduced. Where marked reduction has occurred, the whole muscle has become dorsal and superficial in character, lying mainly lateral to the Vth cranial nerve. The Galbulidae and Bucconidae resemble the Coraciiformes in this respect, but the condition is even more strongly marked, the muscle being vestigial in many species, and absent in some. In typical Piciformes, by contrast, there is generally a well marked medial extension of the origin, as though in compensation for loss of the lateral; the whole muscle is generally more medial and deep in position, lying more or less medial to the Vth cranial nerve.

The factors underlying these differing trends are hard to discern in our present state of knowledge. It is by no means clear why reduction of one part of M. pseudotemporalis superficialis should be compensated by enlargement of another, if, indeed, this is what has actually happened in the Piciformes. A trend towards reduction and loss of the muscle as seen in the Coraciiformes appears more reasonable; it would seem relatively simple for M. add. mand. ext. and M. pseudotemporalis profundus to take over the task of M. pseudotemporalis superficialis in providing adduction force with a component medial to the mandibular ramus. Some answer may eventually emerge from a deeper understanding of cranial architecture.

M. pseudotemporalis profundus and M. adductor posterior

Like M. pterygoideus, M. pseudotemporalis profundus acts both to raise the lower jaw and (through its action on the orbital process of the quadrate) to depress the upper jaw. Relative development of the muscle is hard to assess; its apparent size in dorsal view is certainly a most unreliable guide. In the majority of birds, its excursion is a long one, a fact reflected in its largely parallel-fibred structure; the main exception here is shown by *Tockus erythrorhynchus* in which the muscle is small, with its insertion relatively close to the centre of rotation of the mandible. Otherwise, the most significant variation is the total absence of the muscle in many Alcedinidae. This is certainly related to the form of the skull in this family, in which palatines and pterygoids lie almost in the same plane, and the quadrate has swung backwards (by comparison with other birds), so that the orbital process lies very close to the mandible. Only a small M. pseudotemporalis profundus is therefore possible in any case, and loss of the muscle is not surprising. Even more extreme versions of this skull form are seen in a number of other fish eating groups (Barnikol, 1952), and loss of M. pseudotemporalis profundus has also occurred in some of these, e.g. *Sula, Phalacrocorax* (Hofer, 1950). A similar quadrate shift, accompanied by loss of M. pseudotemporalis profundus has also taken place (though for different morphological reasons) in the Psittaciformes (Hofer, 1950; Burton, 1974*c*). It is interesting to note that the muscle is present in some Cerylinae, but absent in others; detailed observation and comparison of feeding actions in members of this subfamily might produce interesting results.

M. adductor posterior, by reason of its situation so close to the quadrato-mandibular joint and consequent short moment arm, can play little part in adduction, but has been suggested to act in providing support for the lower jaw on the quadrate (Zusi, 1962). It shows relatively little variation among species studied here. The lateral expansion seen in some barbets would somewhat increase its capacity for adduction; this may be a primitive feature (see discussion under M. add. mand. ext.).

M. pterygoideus

Because this muscle is attached at one end to the mandible, and at the other to the palatal complex, it acts both to raise the lower jaw and to retract the palate and thus depress the upper jaw. The siting and structure of components of the muscle may favour one or the other of these two main actions, and functional accounts of M. pterygoideus inevitably concentrate on these two aspects. Although an analysis in these terms goes part way to explaining the structural complexity of the muscle, it leaves a number of questions unanswered in the case of the Coraciiformes and Piciformes. Satisfactory answers will probably require a much more detailed understanding of jaw mechanics than we at present possess.

Particular interest centres on the division of M. pterygoideus dorsalis into lateral and medial portions, and on the modifications of each. Two families examined (Upupidae and Phoeniculidae) showed no division into two portions; nor does *Ramphastos toco* (Ramphastidae). All but one of the remaining families have the muscle divided by a groove into which N. pterygoideus passes, shortly after diverging from the mandibular ramus of the Vth cranial nerve. The exception is the Bucerotidae, in which a clear groove divides the muscle, but the nerve penetrates it an appreciable distance posterior to the groove. (If the raphe of the bipinnate M. pter. dorsalis in *Phoeniculus purpureus* is considered homologous with the dividing groove, then this genus shows a similar condition). A similar situation was found among the Charadrii studied by Burton (1974*a*). A reasonable explanation for such a dichotomy would be to regard the undivided condition as primitive, and the two positions of nerve relative to groove as alternative derived conditions; however, the possibility cannot be excluded that a divided condition may return to an undivided one. Even less clear is the functional relevance of the division.

Physical separation by a groove implies that these two parts of the muscle perform quite distinct actions. M. pter. dors. lat. is oriented more nearly parallel to the long axis of the skull, and hence would act more effectively as a depressor of the upper jaw; at the same time, its more anterior placement on the mandible would improve its capacity for adduction. M. pter. dors. med. seems badly situated from both points of view; in the case of the passerine genus *Loxops*, Richards & Bock (1973) suggest that it functions mainly to rotate the pterygoid (to which it is largely attached) during kinesis. However, in many of the birds examined in this study, M. pter. dors. med. extends far onto the palatine, and may be so oriented as largely to overcome its disadvantageous position for palate retraction. In such cases, the muscle is functionally almost equivalent to a completely undivided M. pter. dorsalis. Groups showing this condition of M. pter. dors. med. may have M. pter. dors. lat. attached to the maxillo-palatine (see below) or much reduced, as in the Galbulidae. In some Galbulidae, M. pter. dors. lat. is approaching a vestigial condition, and interestingly, one of them (*Jacamerops aurea*) shows a partial division of M. pter. dors. med. in a similar situation to the groove which divides M. pter. dors. lat. from M. pter. dors. med. in the majority of birds. (Total loss of M. pter. dors. lat. would leave N. pterygoideus in the curious situation of entering the muscle via its anterior edge.) The evolutionary reasons for this development remain obscure, and do not seem to be correlated in any obvious way with changes in skull architecture. The Bucconidae generally resemble the Galbulidae in the narrowing and reduction of M. pter. dors. lat., yet one of them (*Chelidoptera tenebrosa*) surprisingly retains a M. pter. dorsalis divided by a groove in the normal position.

A feature of much interest revealed by this study is the attachment of M. pter. dors. lat. to the maxillo-palatine in several families. This feature has not been previously described in any bird, even in Starck's (1940) study of the Bucerotidae. Attachment to the maxillo-palatine was found in the Alcedinidae (excluding the Cerylinae), the Phoeniculidae, Bucerotidae, many Capitonidae and Ramphastidae. The significance of this modification is not immediately clear. The maxillo-palatine may simply act as a useful additional surface for muscle attachment, permitting the development of a bulkier M. pter. dors. lat. However, it should be noted that by attaching on the maxillo-palatine, M. pter. dors. lat. depresses the upper jaw directly, and not via the medium of the palatal complex. It is possible that such a fundamental innovation may have other advantages than simply to increase the force for adduction of the lower jaw and depression of the upper. Possibly a careful comparative study of jaw movements in related birds differing in this feature (similar sized members of the Daceloninae and Cerylinae would be highly suitable) might shed further light on this point.

It may be noted that the presence of a bipinnate M. pter. dors. lat. is not correlated with attachment on the maxillo-palatine, although both features occur together in most Alcedinidae and the Bucerotidae—and in *Phoeniculus purpureus*, in which the bipinnate structure of the entire M. pterygoideus dorsalis is functionally equivalent to that of M. pter. dors. lat. alone. Other groups in which bipinnate structure occurs are some Momotidae and Indicatoridae, and more moderately in the Picidae (except *Picumnus* and *Jynx*). The feature might be expected to relate to a need for powerful contraction over short distances, as when the extent of jaw opening is small, or in isometric contraction with the jaws held open. Small amplitude jaw movements are probably important in many kingfishers and woodpeckers, and maintenance of a position with jaws slightly parted may be essential during drumming or chiselling by woodpeckers (Spring, 1965; Bock, 1964, 1966). Prolonged isometric contraction would also seem to play a part in manipulation of large fruits by some hornbills, though toucans face similar problems and do not have a pinnate M. pter. dors. lat.

Finally, the retractor palatini slip of M. pter. vent. med. requires comment. Among the groups considered here, this feature occurs only in the Upupidae, Phoeniculidae and Bucerotidae. However, a similar modification is found also in many passerines (e.g. Fiedler, 1951; Bock, 1960) and some other orders (Burton, 1974*c*). The families showing the feature here differ from others in the sheer size of the retractor palatini slip, and in its extensive attachment on both palatine and pterygoid; it appears to comprise all of M. pter. dors. med. post. plus part of M. pter. vent. med., whereas in passerines, M. pter. dors. med. post. remains (at least partly), in unmodified form (see Richards & Bock, 1973). (The presence in *Tockus erythrorhynchus* of a raphe similar to Ap. N is a further point of difference.) The retractor palatini differs from all other parts of M. pterygoideus in that its action is purely to retract the palate and depress the upper jaw; it cannot adduct the mandible at all, nor can it bring about mandible howing as described by Yudin (1961), Zusi (1962) and Bühler (1970). Thus, it would be of great importance in any feeding action for which independent operating of the upper jaw was required. Small manipulative actions in long-billed birds are probably often of this type (Burton 1974*a*), and its presence in the Upupidae and Phoeniculidae may be related to such needs in these probing feeders. (But note that there is no retractor palatini in the many Scolopacidae which employ a combination of deep probing and skilful manipulation in feeding; their rhynchokinetic upper jaws are more than adequate to meet these needs.) The Bucerotidae obtain their food in a variety of other ways, but their retractor palatini may be a heritage from ancestral forms possibly rather similar to the Upupidae and Phoeniculidae.

M. protractor quadrati et pterygoidei

The action of this muscle is to pull the pterygoid forward and medially, and to rock the quadrate forward and upward about its articulation with the cranium. These movements are communicated to the upper jaw, causing it to be raised.

Noteworthy development of the muscle occurs in the Upupidae and Phoeniculidae; and in the Picidae. In the former two families, the condition of M. protractor is almost certainly related to their probing habits. These two families also have a large M. depressor mandibulae attached to a long retroarticular process. Both features are adaptations for 'gaping', i.e. opening the bill against the resistance of a substrate in order to excavate a wider hole in which to seek prey. Similar modifications are seen in some Charadrii, e.g. *Scolopax* (Marinelli, 1928; Burton, 1974*a*) and a variety of Passeriformes, e.g. the Icteridae (Beecher 1953*a*) and Callaeidae (Burton, 1974*b*). Among the Piciformes, enlargement of M. protractor is presumably connected with its function as a shock absorber during hammering as proposed by Beecher (1953*b*, 1962) and Spring (1965). It is of considerable interest to note that the muscle is not enlarged in *Jynx*—a point which will be discussed further in the systematic review later in this paper.

Some confusion has arisen concerning M. protractor in the Bucerotidae, apparently as the result of a misunderstanding. Hofer (1950), referring to Starck (1940) in a footnote on p. 438 says 'Dass ein M. protr.pterygoidei bei *Buceros* fehlt, ist auffällig und verlangt eine erneute Untersuchung anderen Bucerotiden.' However, Starck makes it quite clear that *Buceros* does possess a M. protractor, a fact which I have checked on a specimen of *B. rhinoceros*: Hofer's misinterpretation apparently arose from Starck's remarks on the muscle treated here as the retractor portion of M. pterygoideus. It is unfortunate, however, that no spirit specimen of *Rhinoplax vigil* was available. The extraordinary kinetics of this bird have been clarified by the very detailed osteological study of Manger Cats-Kuenen (1961), but it would be of great interest to examine its jaw musculature also, especially M. protractor.

Differentiation into two clear parts appears largely to be connected simply with the extent of development of the muscle as a whole. A more puzzling aspect is the extent of attachment to the orbital process. In most birds considered here, attachment on the quadrate was limited mainly to the body and mandibular process, but there seems to be no obvious common feature separating these from the species in which extensive attachment on the orbital process was found. It may be relevant to note that fibres attached on the postero-medial side of the orbital process are directly antagonistic to M. pseud. prof., attached on its antero-lateral surface. Injury to the orbital process caused by M. pseud. prof. can occur (Burton, 1972), and possibly a better understanding of this point may be achieved by more detailed study of the action of these two muscles as a paired and antagonistic unit.

M. depressor mandibulae

M. depressor acts to depress the lower jaw; it probably also plays a part in elevating the upper jaw, through its upward force component on the quadrate (Bock, 1964; Zusi, 1967; Bühler, 1980). The connection between enlargement of this muscle and the 'gaping' method of excavating food has been noted above under M. protractor. Among the Coraciiformes and Piciformes, such enlargement occurs only in the Upupidae and Phoeniculidae, with some indication of a retroarticular process also in the Bucerotidae. The fact that M. depressor is not markedly enlarged in the Picidae supports the view that the great development of M. protractor in this family is unconnected with gaping.

Tongue, hyoid, and hyoid musculature

Tongue and hyoid skeleton

The tongue is greatly reduced in the Alcedinidae and Upupidae, and very small also in the Phoeniculidae and Bucerotidae. In the Alcedinidae, this reduction is presumably related to the consumption of fish; several other groups of fish eating birds show similar tongue reduction, notably among the Pelicaniformes and Ciconiiformes. Clearly, a long tongue would be ineffective in manipulating such relatively large and slippery prey, but the small structure which is retained is fully functional, and presumably aids in swallowing. It may be noted in passing that although various kingfishers include insects, reptiles and other prey in their diets this is not accompanied by any enlargement of the tongue. On the other hand, groups such as the Coraciidae and some Bucconidae which consume relatively large prey, but not fish, have relatively large tongues.

In the Upupidae and Phoeniculidae, different factors have produced a similar result. These birds include many small insects in their diets, but these are obtained by probing in firm substrates, such as earth or wood. Their decurved bills are strongly reinforced, and for much of their length there is no lumen in which a tongue could be accommodated. Similar factors have led to tongue reduction in some shorebirds, e.g. *Numenius* (Burton, 1974*a*). The Bucerotidae in general have bills which could accommodate a longer tongue, so their short tongue condition is more difficult to explain; possibly their ancestry included a stage resembling the present day hoopoes. Sheer bill size is certainly no bar to tongue elongation, as the Ramphastidae demonstrate.

The distribution of brush tongues is more puzzling. Tongues with their tips or edges split into laciniae are found in three families of Coraciiformes, in a few Galbulidae and Capitonidae, and in the Ramphastidae. They do not relate in any simple or obvious way with food, as birds showing this feature have diets ranging from small insects through vertebrates to fruit. There is obviously much scope for further investigation of this feature, and not only within the orders considered here. The dense small papillae on the basal region of the reduced tongues of the Upupidae, Phoeniculidae and Bucerotidae probably serve to improve their friction grip.

Of all tongue modifications within the two orders, however, the most intriguing is certainly that exhibited by the Picidae. The enormously long 'tongue' in this family actually includes only a relatively tiny horny tongue and entoglossum; the greater part of its extended length consists of the elongated basihyal, and the approximated anterior ends of the ceratobranchials, sheathed in epidermal tissue derived from the buccal floor. The advantage of this arrangement is that a capacity for tongue movement and manipulation is retained even while probing deeply in an insect burrow; if the horny tongue alone were elongated as in many nectar feeders, such as the Trochilidae, its articulation with the basihyal would lie much too far back to allow useful movement within a confined space. An analogy to the tongue extension of the Picidae is seen in the bills of many Scolopacidae, which have the zone of kinetic bending in the upper jaw shifted far forward, so that fine movement is still possible at the bill tip, even while probing deeply (Burton, 1974*a*, Marinelli, 1928).

Although the tongue and hyoid of the Picidae seem at first sight so different in structure from those of their relatives, some indication of how they evolved can still be gained by examining other families of typical Piciformes. Several structural characteristics suggest that among these families the tongue has assumed a role in which forceful protraction and manipulation are of greater importance than in the Coraciiformes, or, perhaps, many other orders. The relatively long, narrow basihyal is one of these, adding considerably to the effective length of the tongue. Such a tongue would be less effective when pushing large food items backwards, by retraction; for this purpose it is better for the basihyal to be short, yet wide enough to provide adequate anchorage for M. stylohyoideus and M. thyreohyoideus, as in the Coraciiformes. The entoglossum is generally more thoroughly ossified than in the Coraciiformes, also suggesting a more forceful role, and in a number of species shows a curious double structure, with anterior and posterior halves connected by a narrow region which is cartilaginous in some. Possibly this makes possible some degree of passive bending which may be useful in prey manipulation, making up in part for the absence of M. ceratoglossus anterior which confers a degree of independent tongue tip bending in many birds. The ultimate development of a very long basihyal and short tongue makes this unnecessary in the Picidae, which show at best only slight indications of the entoglossum shape of their relatives.

Hyoid musculature

M. mylohyoideus

Contraction of this muscle raises the floor of the mouth. The extent of its variation within the Coraciiformes and Piciformes remains unclear, and therefore cannot profitably be discussed at present.

M. ceratohyoideus

This muscle pulls the hyoid horns medially, opposing the lateral force component of M. branchiomandibularis. Its reduced condition in the Alcedinidae is perhaps not surprising considering the feeble development of M. branchio-mandibularis in some members of the family. However, the total loss of M. ceratohyoideus in the Indicatoridae is not accompanied by any reduction of M. branchiomandibularis. In the Picidae, which also lack it, medial movement of the horns is imposed during protraction as they slide forward within a cylinder of tissue derived from the buccal mucosa.

M. stylohyoideus

The main retractor of the tongue, and also capable of deflecting the tongue to one side, by unilateral contraction. M. stylohyoideus is essential if the tongue is to be used effectively for thrusting food backwards in the buccal cavity. An alternative means of propelling food backwards is by means of head jerking, and this is likely to be the most effective method where food items are relatively very large—e.g., fish, frogs or lizards, as consumed by several families of Coraciiformes. Diets of this type are associated with tongue reduction, and it is perhaps not surprising that there is also a tendency towards reduction of M. stylohyoideus in the Coraciiformes. Total loss has occurred in the Bucerotidae, which rely heavily on head jerking to propel food backwards, but its near loss in the Todidae is more unexpected.

M. stylohyoideus also appears to have been lost in the Coraciidae, Galbulidae and Bucconidae, but its place is taken by a slip which is apparently a part of M. serpihyoideus—though possibly a M. stylohyoideus whose insertion has completely shifted to the ventral surface of the hyoid skeleton. This unusual arrangement is certainly a derived character, and its presence in just these three families must inevitably provoke some phylogenetic speculation (see p. 149–150).

M. branchiomandibularis

This muscle is the protractor of the tongue, responsible for pulling it forward to manipulate food or even to capture it, as in woodpeckers. The enormous development of M. branchiomandibularis in the Picidae is obviously essential to bring about the extensive protrusion of which their tongues are capable; similarly its virtual absence in some kingfishers is connected with a vestigial condition of the tongue, which plays little part in food manipulation.

A more intriguing point concerns the surprising variability in its sites of origin, seen mainly among the Coraciiformes. Among birds of other orders and in several families studied here, M. branchiomandibularis originates simply from the medial surface of the mandible. Probably, therefore, this is the normal (=primitive) condition, and origin on the buccal mucosa or mandibular symphysis is a derived feature. If this view is correct, these unusual sites of origin probably arose through gradual anterior extension of the origin along the medial surface of the mandibular ramus. Thus, the Upupidae and Phoeniculidae would represent a transitional stage in a shift of origin to the mandibular symphysis. Origin on the ventral surface of the buccal mucosa is less easy to interpret. This condition usually occurs in combination with attachment on the mandibular ramus, and may simply be another way of gaining an increased area for origin; alternatively, it might have arisen by secondary reduction from attachment at the mandibular symphysis.

Before this interpretation can be adopted with confidence, however, it would be desirable to understand the relation of M. branchiomandibularis and M. genioglossus more fully. The latter muscle is absent in many of the birds studied here, as also in very many other birds. However, where present, its origin is from a ledge at the mandibular symphysis similar to that from which M. branchiomandibularis arises in several families. There is no correlation between the presence of M. genioglossus and any particular state of M. branchiomandibularis. Nevertheless, it is possible that the presence of an M. genioglossus was a necessary condition for the shift of M. branchiomandibularis origin to the mandibular symphysis, even if M. genioglossus itself has subsequently been lost. If so, forms showing spread of M. branchiomandibularis origin onto the mucosa only may have developed their extension of origin subsequent to loss of M. genioglossus. A further possibility which cannot be discounted is that a muscle resembling M. genioglossus could arise *de novo* from M. branchiomandibularis. A condition which could conceivably serve as a preliminary state for such an event is seen in the Todidae; the medial slip of this muscle would only need to lose its attachment to the epibranchiale to become indistinguishable from M. genioglossus. Much more study of these and other birds will be required to clarify the relation between these two muscles, and such study should certainly include close examination of their ontogeny.

Variations in siting of the origin of M. branchiomandibularis also prompt speculation as to their functional significance. Forward extensions of origin obviously result in a longer muscle, and therefore, potentially a greater capacity for tongue protrusion. However, this is of little value without enlargement of the tongue and hyoid skeleton, and in practice birds which do show modifications for extensive tongue movements (such as the Picidae, or nectar feeders, notably the Trochilidae) have achieved these almost entirely by lengthening the hyoid horns, and thus the insertion of M. branchiomandibularis. Alternatively, the use of new sites of origin might have arisen simply to enlarge the muscle as a whole, and hence its potential force. This is also an unsatisfactory explanation, since the space available for insertion on the epibranchiale sets a limit on the bulk of the muscle; moreover, many of the birds possessing an anteriorly sited origin have small tongues for which forceful action seems unnecessary. This problem must remain unresolved at present, but further study might well consider the possible significance of the change of plane which has resulted from change in origin. The horizontally flattened M. branchiomandibularis seen in birds with an origin on the mandibular symphysis or buccal mucosa may have important effects on the floor of the buccal cavity itself, additional to its action in tongue protraction.

M. genioglossus

An effect on the buccal cavity is a possible action of this muscle; Bock and Shear (ms., mentioned by Richards & Bock, 1973) suggest that the pair of Mm. genioglossi act as a set of guides along which the tongue slips as it is protruded. Whatever its functions, any clarification of them which results from future work may also provide some explanation of modifications of Mm. branchiomandibularis, as discussed above. Since so many birds lack M.

genioglossus, it may be that even in some which possess it, the muscle no longer has any biological role, and merely awaits the genetic changes necessary to bring about its total loss.

M. ceratoglossus

This muscle depresses the entoglossum, and with it the tongue, relative to the basihyal. It is a short-fibred, unipinnate muscle, capable of exerting substantial force; this is particularly so in those birds which have enlarged the area for fibre origin by extending onto the basihyal. This feature occurs in the Indicatoridae, Capitonidae and Ramphastidae, and in the two latter at least may be related to a need for powerful manipulation of fruits and other large food items.

M. ceratoglossus anterior and M. hypoglossus medialis

These two small muscles, where present, act via the median aponeurosis to depress the tip of the horny tongue relative to its bony or cartilaginous base; M. hypoglossus medialis can also act (like M. ceratoglossus, s.str.) to depress the tongue relative to the basihyal. Their distribution in birds generally is patchy and difficult to explain. Among those reviewed here, they occur mainly in insect eaters, notably the Meropidae and Galbulidae; they may thus be of some value in the manipulation of insect prey, particularly the potentially hazardous venomous Hymenoptera which both consume.

However, the biological roles of these muscles cannot be reliably discerned until their evolutionary history has been clarified. Both muscles appear to have a scattered distribution amongst a variety of birds of several orders, suggesting that their presence is a primitive feature. Against this, they are relatively simple structures, probably derived from neighbouring muscles, and performing a distinct action not duplicated by other muscles. Consequently, they might have appeared independently in unrelated groups, or might even reappear secondarily after an initial loss. This question could very likely be solved by checking for these muscles in a much wider range of birds than so far studied; a more comprehensive picture of their distribution might reveal some significant pattern. It must be remarked that such a search would need to re-examine many groups whose tongue musculature has already been studied, as they have certainly been overlooked in some accounts, possibly due in part to nomenclatural confusion.

M. hypoglossus obliquus

Contraction of this muscle depresses the posterior end of the entoglossum. If right and left muscles contract together, the tip of the tongue will be raised, but unilateral contraction will also deflect the tip of the tongue to the ipsilateral side. Unilateral action is presumably possible only in muscles of Type 2; where right and left have merged into a continuous loop (Type 1), elevation of the tongue tip is the sole function of the muscle. Only the Todidae showed the Type 1 condition in the groups studied here; probably their small invertebrate prey require little reorientation prior to swallowing, and lateral tongue movements may thus be of less importance.

The modified elongated form of Type 2 seen in the Upupidae, Phoeniculidae and typical Piciformes is of special interest. Because of the considerable length of M. hypoglossus obliquus in these birds, a large part of the muscle is oriented at only a very small angle to the basihyal. Where insertion is made via an aponeurosis as in the Indicatoridae and Picidae, individual fibres may be oriented more steeply to the basihyal, but the line of action of the whole muscle is nevertheless very nearly parallel to the basihyal. Thus, although the muscle as a whole may be much larger (and therefore capable of exerting more force) than in the normal condition, its range of action may be more limited. This is simply because a fibre (or aponeurosis) attaching on the paraglossale cannot elevate the tongue past the point at which the two are in line; only fibres situated well anteriorly are able to raise the tongue tip appreciably above the axis of the basihyal. The modified form of Type 2 will thus do little more than to bring the tongue into line with the basihyal, and even its range of lateral action will be more limited. It will still, of course, be essential for returning the tongue from a depressed position (as brought about by M. ceratoglossus), but this provides no explanation for the evolution of the elongated form of the muscle.

The importance of this modification probably lies in its effect when contracting synergically with M. ceratoglossus. The two muscles will then provide a strong backwardly directed force on the tongue both above and below its pivot on the basihyal tip. In this state, tongue and basihyal form a single rigid unit, capable of forceful probing actions. Such an arrangement was doubtless a crucial preadaptive condition permitting the evolution of the highly adapted probing tongue of woodpeckers. This differs from those of other Picidae principally in its relatively much longer basihyal, producing an M. hypoglossus obliquus so long that it appears exactly like a dorsal version of M. ceratoglossus—hence the term 'M. ceratoglossus superior' used by Leiber (1907*a* & *b*). The factor triggering this transformation must simply have been the abandonment of virtually all forms of diet other than those obtained by tongue probing, and consequently the abandonment of the more versatile tongue which other typical Piciformes still retain. It is probably significant that the nearest approach to the M. hypoglossus obliquus of the Picidae is shown by the Indicatoridae, which have a narrow diet including many insect grubs, for which forceful tongue probing may be an important feeding technique.

M. tracheohyoideus and M. tracheolateralis

Much interest attaches to the pattern of distribution of the two alternative sites of origin of M. tracheohyoideus, which acts as a retractor of the tongue and trachea. The simplest explanation for the distribution found is to suppose that origin on either the midline or laterally on the clavicle are both derived conditions, the primitive situation (represented here only by the Bucerotidae) being that in which both sites are utilized. If this view is correct, a shift from one site to the other seems unlikely and this dichotomy is therefore of considerable phylogenetic significance (pp. 423 & 430). The generally small amount of variation in M. tracheolateralis seems, by contrast, to be of no great interest.

M. thyreohyoideus

This muscle retracts the tongue relative to the larynx. Within the Coraciiformes and Piciformes it shows little variation requiring comment, save to remark that its great length in the Picidae is a simple consequence of the elongation of the basihyal in that family.

The neck

Cervical vertebrae

Many of the structural variations noted are probably of only minor significance. Thus, the reduction or loss of fused ribs in the Bucerotidae and Picidae, though a derived feature, must surely have occurred independently in the two families. Similarly, the bony struts connecting costal or transverse processes with the lateral crest may well be a primitive feature, but their gradual reduction must have proceeded independently in many families.

Fusion of the first and second vertebrae in the Bucerotidae is of some interest. This feature, which seems to be virtually unique among birds, presumably provides more firm support for the relatively heavy head and bill, but there are many other groups of birds which face similar problems but lack this modification. Beddard (1898) found the same feature in a specimen of *Chunga,* probably the one in the British Museum (Natural History) registered 1870–10–5–1, which does indeed show such fusion. However, another specimen of the same species (*C. burmeisteri*) has the atlas and axis quite separate, as do specimens of the closely related *Cariama cristata.*

Beddard (1898) discussed the significance of a subvertebral canal (as seen in the Picidae) at some length. Outside the Coraciiform/Piciform assemblage it also occurs in the Podicipediformes, Pelecaniformes and Ciconiiformes. Although the canal encloses the carotids, it seems unlikely that it is necessary for their protection. More probably, its value lies simply in the increased area which it makes available for attachment of the fleshy slips of the highly developed M. longus colli ventralis. It is interesting to note that there is some development of a subvertebral bridge in *Jynx* and even in *Indicator,* perhaps denoting an early stage in specialization for excavation.

Cervical musculature

Excellent discussions of the actions of the neck muscles and some factors which have influenced their evolution in *Rynchops nigra* are given by Zusi (1962). Comparative accounts for the Charadrii and the Callaeidae (Burton, 1974*a* & *b*) provide further information on the functional significance of various structural modifications. However, many problems concerning their evolution remain to be answered. An issue of particular importance has been raised by a recent study of Charadriiform phylogeny (Strauch, 1978). In this numerical investigation, Strauch utilizes data on neck muscle attachments obtained from my earlier study (Burton, 1974*a*). In processing this information, he makes the assumption that evolutionary changes in points of origin or insertion involve only loss of attachments, not gains. This may well be a reasonable working hypothesis. It is certainly true that among birds as a whole, large numbers of neck muscle attachments (and large numbers of vertebrae) are found mainly in groups considered to be of relatively ancient origin (e.g. Podicipediformes, Anseriformes), while they are markedly reduced in more recent groups such as the Passeriformes, or the families studied here. Moreover, the genetic and developmental processes by which cervical muscles might evolve additional origins would seem to be different from those required for most other muscles; extension of origin for a cervical muscle requires that a gap be crossed between one vertebrae and the next. Jaw or tongue muscles, by contrast, could evolve a larger origin by a series of small expansions over a continuous bony surface, e.g., the temporal surface of the skull for M.add.mand.ext.rost.temp. Nevertheless, the possibility that cervical muscles may sometimes evolve additional sites of origin should not be entirely discounted.

Among the birds studied here, a case in point concerns the origins of M. complexus among the Alcedinidae. No other birds, of any order previously investigated possess such posteriorly sited slips of origin; vertebra 6 is the posterior limit in most groups, and many species have an M. complexus originating no further back than 5, or even 4. Previous to this investigation, the only reported exceptions were in *Spheniscus demersus* (Boas, 1929) and *Tryngites subruficollis* (Burton, 1974*a*), both of which have attachment on 7. Kingfishers, however, have attachment at least as far back as 7, and on 8 or even 9 in the Alcedininae.

A scattered distribution among unrelated groups like this is often an indication of a primitive feature. Paradoxically, however, the situation within the Alcedinidae alone seems to suggest just the opposite. The extra sites of origin appear of obvious adaptive value in enabling M. complexus to cope with the heavy head and bill which are a specialized feature of the family. Moreover, the greatest posterior extension is seen in the Alcedininae, which are highly specialized fishers, and not in the more primitive and generalized Daceloninae. On such evidence, the simple explanation would be that the extra origins are also a derived feature, evolved *de novo* for functional reasons. If, on the other hand, they are indeed a primitive feature, it may be supposed that they were more widely distributed among birds at the time the Alcedinidae evolved; thus, their retention in this one family would be due to their specialized role, while the majority of birds, lacking the same needs, have lost them.

Similar problems arise with several other neck muscles whose sites of origin vary in an apparently functionally significant way (see M. splenius capitis, below, and Burton, 1974*a*), and a full answer will require much more knowledge of the genetic and developmental mechanisms controlling them. Such further research might initially be best concentrated on *Gallus gallus*, or some other domestic bird whose genetics and embryology are already well known.

M. biventer cervicis

This muscle acts both to tilt the head upwards on the atlas, and to straighten sections I and III of the neck and flex section II upwards. Unilateral contraction would tend to turn the head to one side, but this effect would be very limited except in groups which have the insertions of right and left muscles separated by a wide gap.

The very marked enlargement of M. biventer in the Alcedinidae is undoubtedly connected with the need to maintain posture of the relatively heavy head, which may often be further burdened with a bulky item of prey. Working synergistically with the ventral neck muscles, the muscle may also have an important role in stabilizing head attitude while diving. The role of the transverse aponeurosis between right and left muscles is obscure. It would act to limit unilateral action, or to prevent spreading of the anterior bellies, but why these functions should be needed is unknown. Its distribution within the family is equally enigmatic, since it occurs throughout a group of specialized fishers (the Cerylinae), but also in a scattering of relatively primitive forest dwelling forms among the Daceloninae.

M. biventer cervicis is also noticeably enlarged in *Jynx* and *Indicator*, a fact which may be connected with their habit of excavating for insects and their larvae. However, specialized excavators such as the Upupidae, Phoeniculidae and Picidae generally show reduction of M. biventer. In the Picidae at least, this is probably because much of the task of delivering blows has been transferred to the pelvic musculature, the neck functioning chiefly as a rigid support for the head—a point discussed further under M. longus colli ventralis.

M. biventer is weak also in the Galbulidae and Meropidae, but left and right muscles are separated by a considerable gap at their insertion on the relatively wide cranium. They are thus situated well out from the pivot of atlas and occipital condyle, an arrangement which may help to modify or control lateral head movements of these highly manoeuvrable aerial feeders (see Burton, 1977*a*).

M. spinalis cervicis and M. splenius colli

These muscles together act to straighten sections I and III, flex section II upwards, and raise I and II relative to II and III. Unilateral action will also bring about lateral bending. Although there is some variation in site of origin, particularly of M. splenius colli, this does not appear to fall into any significant pattern.

M. splenius capitis

This muscle acts to tilt the head upwards, and if contracted unilaterally, to turn it to one side as well. Where origin from 3 is present, the fibres involved should exert a greater torque, since they are farther from the pivot of the cranium, and are therefore likely to be important for actions requiring the exertion of large forces.

Among those with attachment only on 2, the muscle is most notably enlarged in the Galbulidae—a feature related, perhaps, to their adroit aerial manoeuvres during the pursuit of prey. Enlargement in this family is made possible by the very extensive occipital area available for insertion.

The utilization of 3 as an additional site of origin in *Phoeniculus* and *Tockus* also makes possible a more bulky muscle. Combined with the greater torque of the posterior fibres, this origin may be important for the excavation techniques of the former, and control of the relatively large head in the latter. In the Charadrii (Burton, 1974*a*), there is a rough correlation between presence of an origin on 3, and the use of probing or other vigorous feeding techniques. Nevertheless, there are many exceptions to this relationship, as also among Coraciiform and Piciform birds; for instance, *Upupa* and many kingfishers might equally seem to have a need for this modification. As in the case of M. complexus, Strauch (1978) regards M. splenius capitis origin on 3 as a primitive feature, and this is probably correct. Thus, its distribution could be explained by assuming that retention would be more likely in lines for which this extensive origin acquired a special biological role relatively early; while those lines which lost origin on 3 before such a role appeared, have been unable to evolve it again. However, as in the case of M. complexus, the possibility of extra origins arising *de novo* cannot be discounted in the present state of our knowledge.

Mm. pygmaei

These muscles act to flex section I of the neck upwards. Their small size, patchy distribution and frequent asymmetry combine to suggest that they are of little adaptive value among the birds studied here, and are being gradually eliminated. Obviously, their presence is to be regarded as a primitive feature, and hence of no taxonomic significance. It is interesting, however, to note in passing that of the five families possessing them, four are considered to share a common origin in the phylogeny proposed in the conclusion to this paper.

Mm. ascendentes cervicis

The actions of this series of muscles are similar to those of M. spinalis cervicis, with additional capacity for lateral bending. They appear to lack significant variation in structure among the species studied here.

M. longus colli ventralis

This large and complex muscle plays a major role in downwardly directed movements of the neck, flexing sections I and III, and straightening section II. The short anterior slips have an independent action on section I. A general pattern seems to emerge of greater emphasis on the short slips among birds whose feeding actions involve relatively small forces, and greater development of long slips among birds with vigorous feeding techniques, such as hoopoes, kingfishers and woodpeckers. However, the relation is far from clear cut, and much more detailed study of this muscle is obviously needed. The most extreme modification of M. longus colli occurs in the Picidae, with short slips eliminated, and very broad and strong tendons for attachment of the long slips. This is, in fact, the only really notable specialization of neck musculature seen in this family, despite repeated loose statements in the literature referring to the highly developed neck muscles of woodpeckers. Its role in the Picidae is evidently to maintain the neck as rigidly as possible in a downward flexed position during hammering, the actual force of the blows being imparted to a large extent by movements of the entire body. Doubtless M. longus colli works synergistically with dorsal neck muscles in maintaining this rigidity, but it is the muscle primarily responsible for resisting the upward bending forces resulting from interaction with the tree trunk.

M. flexor colli brevis

Bending section I upwards is the principal action of this muscle; unilateral contraction will also produce lateral bending. The small variations in structure observed are probably of little adaptive significance.

M. flexor colli profundus

The action of this small muscle supplements those of the anterior slips of M. longus colli ventralis, and it is probably subject to similar selective forces. However, as explained under M. longus colli, the factors underlying the balance between long and short slips will not be adequately understood until much further study has been carried out.

M. complexus

The principal action of this muscle is to tilt the head upwards. Once upward tilting of the head has reached its limit, further contraction will straighten section I. Unilateral action will turn the head and bend section I sideways. A further action is possible if the muscle has origin posterior to section I; it is then capable of raising section I relative to section II. Among the Coraciiformes and Piciformes, only the Alcedinidae possess this ability, with slips of origin as far back as 8, or in one individual *A. atthis,* 9. The muscle is also strikingly bulky in this family.

Kingfishers have relatively very large heads, and their prey are often heavy. Presumably the large M. complexus provides a major part of the force necessary to maintain head posture. Its origins posterior to section I may indicate that in many actions, head and section I maintain a constant configuration, and are moved as a unit on section II. The extra length of M. complexus in kingfishers may also be advantageous in holding head and neck firmly in line when diving. An M. complexus ending at 5 or 6 would act at a less favourable angle for maintenance of head posture in the extended position, though the difference would be much less marked in the perched position, with head horizontal. The relatively short necks of kingfishers exagerrate this effect.

As discussed earlier, it would be of great interest to know whether the extensive origin of M. complexus in kingfishers is a primitive or a derived feature. If genuinely primitive, then this may have been a key factor enabling the family to evolve their fishing adaptations. An allied question, discussed in the systematic review, concerns whether the fishing behaviour itself is primitive in the group or not.

Woodpeckers have a comparatively small M. complexus. This is perhaps not surprising, since in this family, the head is kept flexed downward for much of the time whilst foraging, and the main emphasis is on the ventral cervical musculature (see under M. longus colli).

M. rectus capitis superior

Contraction of this muscle flexes the head and section I downwards. It is generally shorter in the Coraciiformes and Piciformes than in the Charadrii studied by Burton (1974*a*), but little significant variation was encountered in the species studied.

M. rectus capitis lateralis

Upward tilting of the head is the primary action of this muscle; unilateral contraction will contribute to turning the head and bending Section I sideways. Its actions serve only to reinforce those of M. complexus and M. splenius capitis, and the muscle shows reduction in many species studied here. Extreme reduction of the muscle, as in the Galbuloidea, has not previously been reported in other birds, and is presumably related in some way to the large size of M. splenius capitis in this family.

M. rectus capitis ventralis

This is the bulkiest and most important of the muscles acting to tilt the head downwards. It can also bend section I downwards, and where attachment to 6 is present, may act to swing section I downwards relative to section II. Unilateral contraction will contribute to sideways bending. The bulkiness of the muscle in the Picidae is its most noteworthy modification here, a feature clearly related to the need for sustained downward flexion of the head while foraging and excavating in woodpeckers.

Mm. intertransversarii and Mm. inclusi

Though producing some dorsoventral movement, the major importance of these muscles is probably in producing sideways bending of the neck, or in resisting lateral forces. They also contribute to the support of articulations between vertebrae. The level of detail studied here was not sufficient to permit useful comparisons of function between species.

PART 4

Systematic review

Introduction

This final section summarizes characteristic features of the feeding apparatus for each family, and discusses their taxonomic and functional implications. At the same time, it enables problems requiring further study to be pointed out. Discussions of inter-family relationships should ideally, perhaps, be organized to follow the groupings recognized by Peters (1945, 1948). However, the findings of the present study fall into a pattern radically different from Peters' classification, and such a treatment would make a clear exposition difficult. Instead, the fifteen families studied have been arranged into four groups on the basis of feeding apparatus structure. These are:

(*a*) Typical Coraciiformes: Alcedinidae, Todidae, Momotidae, Meropidae, Coraciidae (including Brachypteraciinae) and Leptosomatidae.
(*b*) Hoopoes and Hornbills: Upupidae, Phoeniculidae and Bucerotidae.
(*c*) Galbuloidea: Galbulidae and Bucconidae.
(*d*) Typical Piciformes: Capitonidae, Indicatoridae, Ramphastidae and Picidae.

It may be noted that on the basis of evidence produced by Feduccia (1977), group a. might well have been subdivided. The four group arrangement is retained, however, but Feduccia's proposals are discussed at some length in the concluding sections of this review.

No attempt is made to discuss theoretical concepts in phylogeny reconstruction and classification, but the phylogenetic reasoning followed pays due regard to the points raised by Cracraft (1972).

Typical Coraciiformes

Skull and jaws are highly variable in form and proportions, but always have a complete maxillo-palatine bridge, the quadrate usually with a prominent medial condyle. A post-orbital ligament is present in all but a few Alcedinidae, and the lower jaw has a secondary articulation (medial brace) in all families except the Leptosomatidae. M.a.m.e.rost.lat. is limited in extent, and sometimes vestigial or absent, while the expanded anterior part of M.a.m.e.vent. lies well forward, exposing M.a.m.e.caud. to lateral view. M.pseud.superf. generally has an extensive lateral origin, but its medial region is reduced; NV passes under the muscle towards its medial side, quite near the dorsal surface, with the ramus pterygoidei and ramus mandibularis usually running close together for some distance. The origin of M. pseud.prof. on the orbital process of the quadrate is usually a broad one. M.pter.dors.lat. is rather narrow in many, but sometimes bipinnate in structure, and with attachment to the maxillo-palatine in the Alcedinidae. The tongue varies much in development, but the entoglossum is always largely cartilaginous, and the basihyal fairly short. M.stylohyoideus is reduced in the Todidae and absent in the Coraciidae, but replaced in the latter by a slip from M. serpihyoideus. M. branchiomandibularis takes much or all of its origin from the ventral surface of the buccal mucosa in most species. M. genioglossus is present in the Momotidae, Meropidae and Coraciidae. M. tracheohyoideus originates on the clavicle. Mm. pygmaei are present in some Meropidae, the Coraciidae and Leptosomatidae. Dorsal components of the neck musculature, concerned with raising the head, are particularly well developed in the Alcedinidae.

ALCEDINIDAE

The feeding apparatus shows numerous distinctive features, many of which appear to be related to fish eating. This suggests that fish have for a long time been an important element of diet in the history of this group, even though some species have turned to an entirely terrestrial way of life. Basic feeding strategy in most species is to wait for prey from a lookout point, captures are fairly infrequent, but prey are relatively large. A similar strategy is used by some other Coraciiformes, e.g. rollers, but piscivorous kingfishers face greater problems since their prey are slippery and difficult to handle, as well as large. The long bill with its sharp tomia improves grip on fish. Kinetic coupling of the jaws appears to be reduced in the Alcedininae and some Cerylinae where the postorbital ligament is weak or absent; possibly this facilitates bringing the jaws parallel, giving maximum contact with prey. Jaw adductors are generally well developed, including a pinnate M.pter.lat. which is attached to the maxillo-palatine in the Alcedininae and Daceloninae and the whole head and bill is relatively massive, imparting the characteristic appearance of body form in kingfishers. Apart from the need for a large feeding apparatus to cope with large prey, the heavy head and bill probably also aid correct alignment when diving through water; terrestrial feeding kingfishers show reduced skull weight. Bill length is influenced by prey size, and by the depth at which prey is secured; ecological factors involved would repay close study, e.g. among Neotropical species in which Fry (1970*a*) noted a simple mathematical ratio between bill lengths of species occurring within the same area. The 'elongated' form of the skull, with pterygoids, palatines and jugals lying almost in one plane is another aspect showing adaptation to movement through water and consumption of fish; reduction or loss of M. pseudotemporalis profundus has, however, resulted from the associated reorientation of the quadrate. *Clytoceyx rex,* despite its extraordinary bill shape, shows the same basic skull morphology; this bizarre species would, nevertheless, be worth intensive study in the future, both in the field and the laboratory. A basiphenoid notch (Burton, 1978) present in all Cerylinae and many Alcedininae and Daceloninae, is believed to be a diving adaptation, perhaps related to Eustachian function.

The tongue (of only minor value in fish consumption) is much reduced, the basihyal expanded to form a wide, flat plate. M. ceratohyoideus is feeble, and M. stylohyoideus has anatypical insertion (anterior tip of ceratobranchiale). M. branchiomandibularis has an entirely mandibular insertion in the Alcedininae and Cerylinae, but is generally reduced in some smaller species. M. hypoglossus is feeble. The neck musculature shows remarkable development of head extensors, particularly M. biventer and M. complexus, providing the extra force needed to support or stabilize the heavy head when handling prey or diving.

Taxonomic problems within the family are for the most part at species or genus level, and anatomical studies are of limited value in resolving them; the basic division into three subfamilies is well supported by this study. The Cerylinae fall into two groups clearly separated by presence or absence of M. pseudotemporalis profundus. Lack of the muscle is obviously a derived character, possession a primitive one; however, those with the muscle appear to form a more closely related group, sharing generally large size and plumage similarities. Conversely, absence of the muscle may have been derived twice; Fry (pers. comm.) considers Neotropical forms (*Chloroceryle* spp.) probably not closely related to *Ceryle rudis.* The relationship of *Tanysiptera* to other Daceloninae may be worth further study; in skull form, and some features of jaw musculature (e.g. M. pterygoideus lateralis) it is atypical of the subfamily, and perhaps rather primitive.

TODIDAE

Todies feed on small flying insects close to fairly low foliage and their wide flat—yet long—bills, with strong rictal bristles obviously facilitate this. They are tiny birds and some of their structural features are no doubt related to small size. This is no doubt true of their general simplicity of jaw muscle structure, and especially the reduction of M.add.mand.ext.rost.-temp.—a feature of many small birds. Reduction or loss of M. stylohyoideus and possession of M. hypoglossus obliquus of Type 1 (alone among the families studied here) may also be size related phenomena. Some other features in the hyoid region are less easy to assess. The basihyal has lateral flanges unlike anything seen in other Coraciiformes or Piciformes, and M. branchiomandibularis has a unique strap like medial slip inserting on the mucosa.

There is a general resemblance to the Momotidae, though perhaps not detailed enough to provide firm support for the proposition that the two families are closely allied (see, e.g. Olson, 1976). However, there is certainly little similarity to the Alcedinidae beyond the features shared by all typical Coraciiformes. Sibley & Ahlquist (1972) suggested, on the basis of egg-white protein studies, that todies were more closely related to kingfishers than to motmots. Structurally there is little to support this idea beyond a superficial resemblance in body form which has certainly been imposed by quite different functional needs.

MOMOTIDAE

Motmots feed among foliage or from the ground, often on fairly large prey. Foraging tactics may include both waiting on a vantage point and active search, sometimes on the ground. In broad features, such feeding behaviour resembles that of some kingfishers, rollers and even puffbirds, but they show distinctive structural features, most obviously the serrated tomia of the bill. This no doubt provides improved grip on prey, but it is not clear why this feature is absent in other birds (particularly Coraciiform ones) with similar feeding habits. Perhaps the serrations appeared as the result of some relatively rare genetic change which has simply failed to occur in most groups. Alternatively, it may be related to specific needs, and a closer study of diet may shed light on these. Soft bodied yet powerful prey such as the Tettigonidae which abound in Neotropical forests might be best handled with serrated bill edges. The extraordinary broad bill of *Electron* provides a further puzzle, and its feeding methods reveal no simple answer; again, a more thorough knowledge of diet may be helpful.

Jaw muscle features agree closely with the general characteristics of the typical Coraciiformes. M.pter.lat. is bipinnate only in *Momotus* and *Baryphthengus*, correlating with generally better developed jaw musculature and more robust bills than in *Electron*. The tongue is long and more or less brush tipped, as in rollers. M. stylohyoideus is present, but inserted posteriorly on the basihyal, and the origin of M. branchiomandibularis is variable—on the mandible, or mucosa, or both. M. genioglossus is present. Neck muscle structure shows no unusual features.

It is unfortunate that no specimens of *Hylomanes* were available for study, and that so little is known about the habits of this bird. Although much larger, it certainly shows some approach to the Todidae in bill and body form, and may be able to shed some light on the origin of the Todies.

MEROPIDAE

The long bills of bee-eaters are a vital safeguard against the stings of the venomous insects on which they often feed, but an unusual feature amongst aerial insect hunters in general. Only the Galbulidae resemble them in this way, and for the same reasons; most birds which capture flying insects have large gapes with wide and often very short bills. The problem of accurately seizing a flying insect with a long narrow bill must be considerable, and elucidation of the adaptations needed to overcome them would make an interesting study. More detailed discussion of this topic as it concerns the Galbulidae is provided by Burton (1977*a*).

Nyctiornis spp. are larger and less aerial bee-eaters which differ from other Meropidae in their relatively shorter but more robust bill, generally more massive jaw musculature, and, interestingly, the lack of Mm. pygmaei. Other bee-eaters show general uniformity of feeding apparatus structure with no significant differences between smaller species which hunt from a perch, and larger ones feeding in continuous flight.

Bee-eaters have broad skulls with a wide occipital region, providing a large moment arm for neck muscles concerned with stabilizing or moving the head. This may be of importance during aerial pursuit, and certainly for the vigorous movements needed to kill and de-venom prey. The postorbital ligament is slender, M.add.mand.ext.rost.temp. is long but very narrow, and M.add.mand.ext.rost.lat. is vestigial. The tongue is long, with a slight brush tip, and M. branchiomandibularis originates on the ventral surface of the buccal mucosa. M. genioglossus and M. ceratoglossus anterior are present.

Bee-eaters and jacamars show many structural resemblances (Fry, 1970*b*) as might be expected from their similar ways of life. Skull form is similar, and M.pter.lat. is markedly narrow in both families—vestigial in some Galbulidae. Both groups (except *Nyctiornis* among the Meropidae) possess a well developed set of M. pygmaei. M. hypoglossus medialis is found only in these two families and the Bucconidae; exactly what this common feature denotes is hard to surmise, however. Many of the resemblances between these two families are, no doubt, due to convergence. However, their origins may not be quite as distant as present classification would suggest—a point which is discussed at length elsewhere in this review.

LEPTOSOMATIDAE

The Cuckoo-roller, *Leptosomus discolor,* resembles *Coracias* spp. in general features of body form and habits, but detailed examination reveals many differences, as Cracraft (1971) found in his osteological study. It is unquestionably correct to classify it in a monotypic family, but rather harder to understand the significance of all its distinctive features. *Leptosomus* evidently originated from an early invasion of Madagascar, well before that which gave rise to the ground rollers, and it certainly retains some primitive features—for example, M. stylohyoideus is present and M. branchiomandibularis unspecialized. However, *Leptosomus* also shows structural modifications which are derived, and in some cases unique. M.add.mand. ext.rost.temp. is surprisingly small, and lacks bipinnate structure; M.add.mand.ext.vent. has aponeurotic attachment to the stout postorbital ligament; M.add.mand.ext.caud. has only one raphe; M.pseud.superf. has a reduced lateral origin. As in the Coraciidae, M.pter.-dors.med. is subdivided into anterior and posterior portions, but in *Leptosomus* the anterior portion is much reduced. M.pseud.prof. has a lateral slip merging with the insertion of M.pseud.superf.; despite the presence of M. stylohyoideus there is an additional slip resembling it from M.serpihyoideus; the tongue is short and lacks any indication of a brush tip.

There are no obvious behavioural factors to account for these features. The Cuckoo-roller's regular consumption of chamaeleons is certainly unusual, but these would hardly seem to require different adaptations from *Coracias* which also feeds on lizards, though of other kinds. The peculiarities of *Leptosomus* may well be associated in some way with its long isolation under conditions of reduced competition and ecological diversity, but much further study will be needed to understand them fully. Further comments on its systematic position will be found in the section on the Galbuloidea.

CORACIIDAE

Ground rollers have been included here, following Peters (1945), but there are good grounds for separating them as a distinct family Brachypteraciidae (Cracraft 1971; Morony, Bock & Farrand, 1976). Reasons for doing so stem, however, from differences in behaviour, plumage and post-cranial anatomy; as Cracraft (1971) found, cranial osteology is very similar throughout, and the present study reinforces his observations.

Eurystomus is the most divergent genus in feeding apparatus structure, with its wide bill and gape adapted for aerial feeding. However, even here, differences are mainly ones of proportion, and in essential features it is very similar to *Coracias* and the ground rollers. All rollers have robust skulls, with very stout postorbital ligament and well developed medial brace. M.add.mand.ext.rost.temp. is large, but M.a.m.e.r.lat. is small or absent, and M.pter. lat. is fairly broad, but of simple structure. M.pter.dors.med. shows division into distinct anterior and posterior portions. Although some large prey, such as lizards, is taken and swallowed whole, there is still clearly a need for effective tongue action in dealing with smaller items, since tongues are relatively long with brush tips, especially in ground rollers. A curious feature of hyoid anatomy is the lack of a true M.stylohyoideus, the slip which replaces it being derived apparently from M. serpihyoideus; the Galbulidae and Bucconidae are the only other families showing this character, although the slip from M. serpihyoideus is present in the Leptosomatidae. M. branchiomandibularis originates mainly on the mucosa. M. genioglossus is present in ground rollers. Mm. pygmaei were found in *Coracias* and *Eurystomus.*

Hoopoes, Wood-hoopoes and Hornbills

Although agreeing with the typical Coraciiformes in some important ways, these three families have many distinctive features of their own in feeding apparatus structure, and appear to constitute a well-marked natural group. The idea of such a relationship has a long, if checquered, history, dating back to Murie (1873), and receives some support from the egg-white protein studies of Sibley & Ahlquist (1972). Some of the shared features appear to be primitive, but undoubtedly most are derived ones associated with specialized methods of using the bill. Most sophisticated of these methods is 'gaping', i.e. opening the bill within a substrate to create a cavity permitting access to concealed prey. This technique is well known in various birds of other groups, e.g. Icteridae (Beecher, 1951), Callaeidae (Burton, 1974). In the present study the Phoeniculidae and Upupidae show the same characteristic gaping adaptations—a long retroarticular process, and massive M. depressor and M. protractor. Of the three families, the Phoeniculidae is the only one to show narrowing of the skull anterior to the orbit sufficient to permit a useful view between the open jaws as in *Sturnus* (Lorenz, 1949). Lack of this feature in *Upupa* may be an unavoidable mechanical necessity to provide an adequate brace against forces acting laterally against the very long bill, when probing hard soil. The Bucerotidae, which feed to a large extent on fruit and exposed animal prey, make less use of this technique, but it is certainly used in foraging by some species, and perhaps also in nest excavation; there is generally at least an indication of a retroarticular process, even though M. depressor and M. protractor are not greatly enlarged. Probably the Bucerotidae arose from a stock in which some specialization for gaping and vigorous excavation had already appeared; the Upupidae and Phoeniculidae seem likely to have shared the same ancestry, but diverged later from a group which had carried this specialization a good deal further. Within the Bucerotidae (q.v.), other forms of bill use have appeared, also leading to drastic structural change.

The skull is robust and heavily ossified in all three families, even apart from the Bucerotidae. The postorbital ligament is moderately to very strongly developed, and the occipito-mandibular ligament unusually stout. However, a medial brace is lacking or only weakly developed (Upupidae). The maxillo-palatine bridge is complete, and is fused with the palatines in the Bucerotidae. The medial condyle of the quadrate is not especially prominent.

M. adductor mandibulae externus is of complex structure in the Phoeniculidae; reasons have been advanced elsewhere (p. 408) for considering this structure primitive. In the Upupidae and Bucerotidae, simplified traces of this structure remain. M. pseudotemporalis superficialis departs from the condition seen in the typical Coraciiformes; although its lateral origin is well developed, it is much more bulky in the dorso-ventral plane, so that the trigeminal nerve is deeply buried. This condition is more normal among birds in general, and hence can be considered more primitive than in typical Coraciiformes, or even the Trogoniformes (see p. 437).

Within the three families, an interesting situation exists with regard to M. pterygoideus dorsalis. The muscle shows no division into lateral and medial portions in the Upupidae or Phoeniculidae (although bipinnate in *Phoeniculus purpureus*), while in the Bucerotidae it is divided, but in a different position, relative to N. pterygoideus, from any other Coraciiformes or Piciformes. This suggests that the undivided condition is primitive, and that division has occurred independently in the Bucerotidae. Attachment to the maxillo-palatine is found in the Phoeniculidae and Bucerotidae.

In all three families a retractor palatini portion is developed from the medial region of M. pterygoideus dorsalis. Attaching on the base of the cranium, it acts to depress the lower jaw without at the same time raising the upper. This probably improves control in the manipulation of food objects—probably an important facility for birds with long bills and short tongues. Kinetic coupling of jaw action is evidently possible, with a well developed postorbital ligament, but it is interesting that *Bucorvus* also shows jaw coupling by means of the structure of the quadrate/mandible articulation. This system is permanent, not depending (as with the ligament) on its state of loading. Whether, and how this relates to the strongly predatory habits of the Ground Hornbills, is a matter for conjecture.

Tongue reduction is most extreme in the Upupidae; the Phoeniculidae and Bucerotidae have rather longer tongues rendered distinctive by the numerous barbs in the basal region.

In all three families, the basihyal has a distinctive 'hour-glass' shape. The origin of M. branchiomandibularis is entirely on the mandible, but far anterior. M. genioglossus is present in all three families, with left and right muscles partly or entirely united in the midline. M. hypoglossus obliquus resembles that in some typical Picidae, with entirely separate left and right sides, and origin on the ceratobranchiale in the Upupidae and Phoeniculidae. M. tracheohyoideus has origin on the clavicle, and on the sternum also in the Bucerotidae.

UPUPIDAE

There is a moderately developed postorbital ligament and a weakly developed medial brace. The orbital process of the quadrate is narrower than in the typical Coraciiformes, but broadened at its tip; vestigial basipterygoid processes are well marked. The postorbital and zygomatic processes lie unusually close together, and in consequence M.a.m.e.rost.temp. is small and narrow. M.a.m.e. has a well developed postorbital lobe, but in structure is otherwise fairly similar to that of the typical Coraciiformes, with small M.a.m.e.rost.lat., M.a.m.e. vent. with a wide fleshy insertion on the lateral surface of the mandible and a narrowly inserting M.a.m.e.caud. M.pter.dors is undivided and of simple structure, with N. pterygoideus entering it well posteriorly.

The tongue is extremely short, without basal barbs. Tongue reduction would seem to be inevitable, since the bill lacks any lumen, for most of its length, in which a tongue could operate. This is a consequence of the reinforcement needed for jaws which are used to probe the ground; a similar effect is seen in various other birds which probe hard substrates, e.g. *Numenius* (Burton, 1974). M. stylohyoideus is extremely slender, and the right and left Mm. genioglossi are completely united as a single median muscle. Rather surprisingly, M. splenius capitis has only the usual origin on 2; forceful head movements when probing might have been expected to require extra attachment on 3 as in the Phoeniculidae. The weak M. biventer is also somewhat surprising. There is obviously still a need for detailed observations on feeding techniques in this common and widely distributed bird.

PHOENICULIDAE

The skull is very similar in general form to that of the Upupidae, particularly in *Phoeniculus. Rhinopomastus* has a less robust skull and strongly decurved bill, probably relying less on gaping, and more on the exploration of insect tunnels. The orbital process of the quadrate is rather more slender, and the palatines wider. There is no medial brace. As in the Upupidae, the postorbital and zygomatic processes are close together, with consequent reduction of M.a.m.e.rost.temp. Otherwise, M.a.m.e is of the complex structure postulated as primitive, with a two part postorbital lobe, narrowly inserting M.a.m.e.vent., and a large, laterally expanded m.a.m.e.caud. M.pter.dors. is undivided, (bipinnate in *Phoeniculus purpureus*) and is attached to the maxillo-palatine.

The tongue shows less extreme reduction than in the Upupidae, and is relatively quite long in *P. aterrimus*; probably it is helpful in transporting such prey as beetle grubs back to the mouth while probing wood. The tongue base is studded with barbs, M. stylohyoideus is normally developed, and M. hypoglossus obliquus particularly well developed, its origin extending well back on the ceratobranchiale. Left and right Mm. genioglossi are united only anteriorly. M. splenius capitis has additional origin on the neural spine of vertebra 3—an adaptation for forceful lateral head movements while probing.

The marked differences in bill shape within the family make them an attractive potential subject for a comparative study of feeding behaviour, with which *Upupa* could well be included.

BUCEROTIDAE

The bills of the Bucerotidae are, of course, their most distinctive feature. Long and deep, their shape is well suited to fruit eating, combining adequate reach with the rigidity needed to support heavy objects at the bill tip. A variety of functions other than feeding are also served by the bills of these birds. Their laterally flattened shape renders them suitable for use as a spatula in applying mud to the nest hole, or for splitting off rotten wood where necessary. Adornments of the bill and casque probably serve as species specific social signals, and the bill of the walled-up female may have significant value in intimidating predators at the nest hole. Normally highly pneumatized, the casque is solid in *Rhinoplax*—probably a secondary adaptation providing extra weight to aid in excavation.

Tockus spp. appear the least specialized, and perhaps the most primitive hornbills. Their skulls, though more massive, are not unlike those of *Phoeniculus* spp.; in larger, heavily casqued hornbills, the resemblance is less obvious. Principal differences apart from bill and casque are the extensive temporal fossa, and the fusion of the maxillo-palatine bridge with the anterior part of the palatines. The quadrate is more robust, and more like that of typical Coraciiformes, with stout orbital process and prominent (though more rounded) medial condyle. The postorbital ligament is extremely broad and strong; coupled kinesis, achieved when the ligament is loaded, is probably essential for the deft throwing and catching movements of which hornbills are capable. They are also able to perform remarkably fine manipulation with the bill-tip, for which independent jaw action would seem important; the retractor palatini portion of M. pterygoideus may be of special value in allowing force to be exerted on the upper jaw alone. However, *Bucorvus* has the jaws coupled not only by the postorbital ligament, but by the structure of the quadrate/mandible hinge, and would seem scarcely capable of uncoupled kinesis; nevertheless, it can carefully manipulate prey, and has a bulky retractor palatini.

Powerful adduction is important, for heavy objects may often need to be grasped securely at the bill tip, and some species systematically crush venomous prey. The extensive M.a.m.e. rost.temp. is largely responsible for the force developed by M.a.m.ext., since fleshy insertion on the lateral surface of the mandible is almost eliminated, though Aponeuroses 1 and 3 are very strong. A small postorbital lobe only remains from the primitive form of the muscle seen in the Phoeniculidae. M. pseudotemporalis profundus has bipinnate structure—an unusual feature among birds in general, but perhaps providing more force than a parallel-fibred muscle for small amplitude coupled jaw movements occurring in throwing and catching actions. M.pter.dors. is divided, but well anterior to the point of entry of N. pterygoideus. M. pter.lat. is bipinnate, with extensive attachment to the maxillopalatine, and the retractor palatini portion of M. pter.dors. med. is also bipinnate.

The tongue is relatively short, but well developed, and much barbed at its base. M. stylohyoideus is absent. The origin of M. branchiomandibularis is a median one at the mandibular symphysis, where right and left muscles meet. Left and right Mm. genioglossi are completely united. M. splenius capitis had additional origin on vertebra 3. The extra force this provides for head raising or turning is of obvious value for birds which handle substantial objects deftly but powerfully with massive heads.

It is unfortunate that no spirit specimen of *Rhinoplax vigil* exists. A study of the jaw musculature would valuably supplement the work of Manger Cats-Kuenen (1961), while the neck musculature may well show unusual modification for support of the extraordinarily heavy head. In general, there is a need for a more comprehensive study of the feeding apparatus in the Bucerotidae, to extend the work of Starck (1940) and the present investigation, both of which have dissected relatively few species.

Jacamars and Puffbirds

These two families at present constitute the suborder Galbuloidea of the Piciformes. The most thorough anatomical study supporting this placement is that of J. Steinbacher (1937), though this dealt rather briefly with the Coraciiformes. More recently, Verheyen (1955*b*) retained them in this systematic position after a study of skeletal measurements. However, the present investigation casts very serious doubt on this classification, for in almost every aspect of feeding apparatus structure they share important characters with the typical Coraciiformes and virtually none with other Piciformes. This evidence agrees with the findings of Sibley & Ahlquist (1972) from egg-white protein studies. Common features of the Galbuloidea and the typical Coraciiformes may be summarized as follows:

1. Desmognathous palate.
2. Quadrate with deep and prominent medial condyle, and a broad orbital process having a long medial edge for attachment of the aponeurosis of M.pseud.prof.
3. M.add.mand.ext. having no M.a.m.e.r.lat., an M.a.m.e.vent. which fans out well anteriorly, and an Ap. 3a in M.a.m.e.caud.
4. The condition of M.pseud.superf., which is thin, originating rather high in the orbit, and with its fleshy portion lying mainly lateral to NV. A reduced muscle in many Coraciiformes, it is vestigial in the Galbuloidea and even absent in a few.
5. The largely cartilaginous entoglossum.
6. Very short basihyal.
7. M. branchiomandibularis originating far forward on the mandible, and often with additional origin on the ventral side of the buccal mucosa.
8. M. tracheohyoideus with origin on the clavicle.
9. The presence of Mm. pygmaei in some species.

With the exception of 9, probably all these features can be correctly regarded as derived ones. In addition, the Galbuloidea share two features with individual Coraciiform families; M. stylohyoideus is functionally replaced by a slip from M. serpihyoideus as in the Coraciidae, and M. hypoglossus medialis is present as in the Meropidae. (It may be noted here that *Leptosomus* possesses both the slip from M. serpihy. and an M.stylohy., and also has a well developed M. ceratoglossus anterior, from which M.hyp.med. is probably derived.) The only feature of any note in which the Galbuloidea agree with the typical Piciformes is in their lack of a medial brace providing secondary articulation for the lower jaw; however *Leptosomus* among the typical Coraciiformes also lacks a medial brace.

Despite this evidence conflicting with their present ordinal classification, many characteristics attest to a fairly close affinity between the Galbulidae and Bucconidae themselves. The very long postorbital process and extremely deep medial quadrate condyle lend their skulls a characteristic appearance posterior to the orbit (though resembling the Coraciidae and Leptosomatidae); the great reduction or even loss of M.pseud.superf. is very striking, taking a typical Coraciiform trend to its extreme; origin of M. branchiomandibularis from the mandibular symphysis is otherwise seen only in the Bucerotidae, which are surely only distantly related; the Bucconidae and some Galbulidae have a narrow median groove on the dorsal surface of the tongue unlike anything seen in other families studied; and the replacement of M. stylohyoideus by a slip of M. serpihyoideus, and presence of M. hypoglossus medialis are features otherwise seen only in single families of typical Coraciiformes.

Exactly how the two families arose is a matter for conjecture. The puffbird body form and way of life is almost certainly the more primitive, but no living puffbird appears much like a potential jacamar ancestor. *Chelidoptera* is an aerial feeding puffbird, but its similarity to jacamars in way of life is a secondary and rather superficial one (Burton, 1977*a*). Delving further back, it is interesting to note features shared by the Galbuloidea, Coraciidae and Leptosomatidae. *Leptosomus* is particularly intriguing. Apart from some jaw muscle peculiarities of its own, it shows many similarities to puffbirds, even to its partially zygodactyl feet; had it occurred in South America rather than Madagascar, its present classification might have been very different. I would suggest, tentatively, that the Galbuloidea arose from a stock not far removed from that which gave rise to the rollers and cuckoo-rollers. The position of this group of families relative to other typical Coraciiformes is less clear, and is discussed further in the concluding section on phylogeny.

GALBULIDAE

The long, straight, pointed bill is the most obvious structural characteristic distinguishing jacamars from puffbirds. Its purpose (as in the Meropidae) is undoubtedly to protect vulnerable parts of the head from the stings of venomous insects. The skull is less robust, but with a characteristic profile; the occipital region bulges upwards and posteriorly, and the elements of the kinetic apparatus lie in one plane with the upper jaw, rather as in the elongated skulls of kingfishers though with a normally sited quadrate. As in the Meropidae, whose skulls are similarly shaped, the form of the cranium may be related to the resting attitude with upward pointing bill while waiting for insects.

Suppression of M.pter.dors.lat. is much more extreme than in the Bucconidae, but in *Jacamerops* a partial secondary division of M.pter.dors.med. has appeared. The tongue is long, with slight indication of a brush tip in *Jacamerops.* There is no M. genioglossus. M. splenius capitis is unusually large in the Galbulidae, covering most of the very broad occipital region of the skull. Its role during pursuit of aerial prey is discussed by (1977*a*).

Jacamars are highly uniform in structure; the only aberrant species are *Galbalcyrhynchus leucotis* with its extremely heavy bill, and the large *Jacamerops aurea,* with a comparatively short and heavy bill. Little is known about the former, and its feeding habits certainly deserve study, to clarify the factors underlying its unusual bill form. *Jacamerops* is less aerial than other jacamars, its habits somewhat resembling those of a puffbird. Nevertheless, detailed structure of its feeding apparatus so closely resembles that of others of its family that it seems almost certain that its atypical features are secondary ones. In this it differs from *Nyctiornis,* which is a rough ecological equivalent among bee-eaters, but seems to have diverged early in the history of the Meropidae.

BUCCONIDAE

Puffbirds are more variable in bill form, size and habits than the jacamars, but invariably more sluggish, feeding on the whole less frequently, though often on larger prey. Even the small and highly aerial *Chelidoptera* conforms to this general rule (Burton, 1977*a*). Skulls are generally more robust, and more normal in form. M.pter.dors.lat. varies considerably in size relative to M.pter.dors.med., but is generally larger than in the Galbulidae. The tongue is of moderate length, simple in shape, and with a very strongly marked median dorsal groove. M. genioglossus is present, left and right muscles having a combined origin on the symphysis.

As stated earlier, no living puffbirds give much indication as to the likely origin of the jacamars, and *Chelidoptera*, despite its aerial habits, seems an unlikely candidate for an ancestral form. Small, lower storey flycatcher/gleaner types such as *Nonnula* or *Micromonacha* may be somewhat nearer to the type of bird from which the Galbulidae were derived.

Typical Piciformes

With the Galbuloidea removed, the remaining families of Piciformes form a closely knit and clearly natural group. Differing in numerous ways from the Galbuloidea and Coraciiformes, they share many derived characters of feeding apparatus structure, some of which reach an extreme in the pecking and tongue probing adaptations of the Picidae. Somewhat surprisingly perhaps, the Picidae also stand out by reason of the primitive structure of M.add.mand.ext., which they alone retain.

Typical Piciformes have a quadrate with a long and rather slender orbital process, and a medial condyle which is not especially prominent. None of them possess a medial brace providing secondary articulation for the lower jaw. In the Picidae (including *Jynx*) and Indicatoridae, the junction of pterygoid and palatine has a distinctive form, with the pterygoid extended far anteriorly medial to the palatine, so that the two bones have a large area of contact—an arrangement seen in many passerines, but none other among the Coraciiform/Piciform assemblage. Characteristic features of M.add.mand.ext. seen in the Capitonidae, Indicatoridae, Ramphastidae and *Jynx* include the extensive M.a.m.e.rost.lat., which spreads out ventrally as a wide, thin sheet covering much of M.a.m.e.vent., which itself fans out quite close to the origin. M.a.m.e.caud. usually lacks an Ap. 3a. M.pseud.superf. lacks any lateral lobe, and is situated well into the orbit with the fifth cranial nerve running entirely lateral to it, deeper than in typical Coraciiformes and the Galbuloidea. It often has a medial extension at the origin, overlapping part of M. protractor. M.pter.dors.lat is usually well developed, with attachment to the maxillo-palatine in the Ramphastidae and a few Capitonidae. (Where this attachment is well developed, it is made by a distinct dorsal slip from the muscle, not seen in the Coraciiformes). M.pter.dors.lat. is bipinnate in the Picidae. The Picidae, other than *Jynx*, also exhibit a greatly enlarged M. protractor.

Tongues are generally well developed, and the basihyal is usually a long and fairly slender rod. An extreme is reached in the Picidae where the tongue itself is much reduced, but extended on an enormously lengthened basihyal. Nearly all, other than the Picidae, have an entoglossum of highly characteristic form, with a constriction about half way along its length. It is entirely ossified in some, while in others, the constricted region is cartilaginous, with the anterior ossified region having the form almost of a second entoglossum in front of the first. M. branchiomandibularis originates on the medial surface of the mandible, not far forward—the condition characteristic of most birds. M. hypoglossus obliquus is long, often with origin on the ceratobranchiale, reaching an extreme in the Picidae. M. tracheohyoideus originates on the anterior tip of the keel of the sternum, or the clavicular symphysis, right and left muscles meeting at the narrow point of origin—not separate origins more laterally on the clavicle as in the Coraciiformes and Galbuloidea. M. pygmaei have not been found in any of the typical Piciformes.

Functional or taxonomic problems within the group are best dealt with at family level. As a general comment however, it is worth stressing the significance of tongue action within this group. Tongue manipulation, sometimes in combination with various forms of excavation, has clearly been a major factor in the evolution of feeding specializations within the typical Piciformes. Although tongue movements are extremely difficult to observe and study, the attempt needs to be made if we are ever to understand how their various feeding mechanisms arose.

CAPITONIDAE

Barbets are the least specialized family of Piciformes, yet they show some interesting modifications of feeding apparatus structure that suggest possible ways in which the more extreme specializations of other families originated. For this reason they certainly deserve much closer study.

Fruits predominate in their diets, and their wide, ample bills, sometimes with serrated or notched tomia, are primarily adapted for seizing and gripping them. Barbets all lack a postorbital ligament, though some capacity for coupled jaw action by means of a modified quadrate/mandible hinge seems to exist in *Megalaima.* Independent jaw action may be important where several fruits have to be carried simultaneously (as illustrated in Thomson, 1964). Some are weakly desmognathous.

M.add.mand.ext. conforms closely to the structure characteristic of the typical Piciformes; M.a.m.e.r.temp. is usually extensive, reaching back nearly to the skull midline. M.pseud. superf. has a medial extension at the origin, generally partially overlapping M. protractor, and is bipinnate in some species, sometimes with a distinct bipinnate medial slip. M.pter.dors.lat. is usually extensive, and has attachment to the maxillo-palatine in several species. In *Semnornis,* this attachment takes the form of a distinct and well developed dorsal slip.

The tongue is moderately long, simple in form in most, but with a brush tip in *Capito* and *Semnornis.* Double structure of the entoglossum is generally well marked, though absent in *Lybius bidentatus.* The basihyal is long except in *Pogoniulus.* M. hypoglossus obliquus is also long, though its origin extends onto the ceratobranchiale only in *Pogoniulus*, perhaps in compensation for the short basihyal.

INDICATORIDAE

With their sober plumage, unspecialized bills and horizontal carriage, honeyguides look more like typical passerines than members of the Piciformes. Nevertheless, in feeding apparatus structure they are closely similar to barbets. The skull is less robust, with reduced ossification particularly apparent in the vomer, maxillo-palatines and upper jaw; there is, however, a weak postorbital ligament. Presumably a heavily reinforced skull is unnecessary to cope with a diet of bee grubs and honeycomb.

M.add.mand.ext. is closely similar to that of barbets, with M.a.m.e.rost.lat. expanded across M.a.m.e.vent. as a thin sheet of fibres. M.a.m.e.rost.temp. is moderately developed, M.a.m.e.caud. only weakly pinnate. M.pseud.superf. has a long medial extension at the origin, and is bipinnate in some. M.pter.dors.lat. is bipinnate in some honeyguides, but is not attached to the maxillo-palatines.

The tongue is simple in structure, and moderately long. The entoglossum is constricted at about the middle of its length, with a cartilaginous middle region and ossified tip. The basihyal is fairly short, but M. hypoglossus obliquus very long, its origin extending to the posterior end of the ceratobranchiale as in the Picidae.

Sibley & Ahlquist (1972) suggested on the basis of egg-white protein studies that the possibility of affinity between honeyguides and cuckoos should be investigated. It must therefore be emphasized that the findings of this study provide strong evidence against any such affinity. I have examined feeding apparatus anatomy in a variety of Cuculiformes, and find it to differ extensively from that of honeyguides. On the other hand, the detailed similarities between honeyguides and other typical Piciformes are hard to discount; indeed, judged on some features of palate structure and the much elongated M.hyp.obl., the Indicatoridae may hold the key to understanding the origin of the Picidae (q.v.)

It may be remarked here that *Prodotiscus* spp. differ markedly from other Honeyguides in bill form and, probably, ecology. Unfortunately, study of their anatomy is much hampered by the present lack of anatomical specimens in museum collections. Remedy of this deficiency might lead to a substantial improvement in our understanding of the evolutionary history of the Piciform families.

RAMPHASTIDAE

The most obvious characteristic of toucans is, of course, the huge bill. This seems primarily adaptive to fruit eating, though as with the Bucerotidae, it has acquired secondary signal functions. The mechanism of feeding, however, clearly differs substantially from that of hornbills, since there is no post-orbital ligament (as in barbets), nor any form of kinetic coupling by modification of the quadrate/mandible articulation. Moreover, the tongue, far from being reduced, is very long, with brush tip and edges. Unfortunately, there is insufficient information about the feeding habits of toucans to interpret these facts satisfactorily. It is not known whether, for instance, toucans regularly hold several fruits along the length of the bill—an action for which reduced coupling might be helpful. Fruits are swallowed whole, and use of the tongue does not appear vital for this purpose; however, insects also figure in the diet, especially when young are being fed, and the tongue may then have some important part to play. Swainson's Aracari is recorded as eating flower filaments; the tongue seems well suited for transporting these along the bill, but how widespread the habit may be is unknown.

Bill shape, a doubly desmognathous palate and lack of a vomer distinguish toucan skulls from those of barbets. Otherwise, they are extremely similar, as is the jaw musculature. M.a.m.e.rost.temp. extends less far back in the Ramphastidae, but otherwise differs negligibly from that of the Capitonidae. M.pseud.superf. is of similar form to that of barbets, but is rather more bulky, and bipinnate in all species examined. M.pter.dors.lat. is attached to the maxillo-palatine by a distinct and bulky dorsal slip.

Despite the longer tongue, the entoglossum is very much like that of some barbets, with similar double structure and a narrow midpoint cartilaginous zone. There is a vestigial M. genioglossus in *Selenidera.* M. hypoglossus obliquus is long, its origin including the anterior part of the ceratobranchiale.

The findings of this study leave little room for doubt that the Ramphastidae and Capitonidae are closely related. I see no need even to postulate a common ancestor for the two families; it seems reasonable simply to regard toucans as a specialized group of barbets which have arisen and radiated in South America. They may well be no further removed from the main stem of barbet evolution than, say, *Pogoniulus.* This is not necessarily, however, to advocate merging the two families; the appearance of such a striking innovation as the toucan bill surely requires taxonomic recognition, though perhaps this might be more appropriately at subfamilial level. However, they are for the present retained as a family in the classification proposed at the end of this paper.

The further question arises as to which barbet group might have given rise to the toucans, and it seems that the answer may well lie in their own zoogeographical region. *Capito* and *Semnornis* of the Neotropics are the only barbets in which brush tongues were found, and *Semnornis* shows additional significant resemblances. It possesses an M.pter.dors.lat. in which attachment to the maxillo-palatine is made by a distinct dorsal slip, just as in the Ramphastidae. Furthermore, *S. ramphastinus* shows a striking similarity in colour pattern to some species of *Andigena* and *Selinidera,* while even the plain coloured *S. frantzii* is not unlike *Baillonius bailloni.* Detailed studies of these birds, particularly in the field of behaviour, should produce results of great interest.

PICIDAE

Woodpeckers (Picinae) and piculet (Picumninae) share many highly distinctive structural features, mostly adaptive to the excavation of wood by hammering. Wrynecks (Jynginae), by contrast, lack nearly all of these though all three have a similar highly modified tongue apparatus. This great disparity between Wrynecks and others makes it necessary to enumerate features point by point for the sake of clarity.

1. The skull of *Jynx* is in general unspecialized and light in structure, resembling that of *Indicator*, though showing even more reduction in the palatal region with vestigial vomer and narrowed maxillo-palatines. Other Picidae retain a simplified palatal structure, but the skull is otherwise heavily ossified, with specialized fronto-nasal hinge, pterygoids, quadrate and otic region. Wrynecks and woodpeckers share with honeyguides a distinctive structure of the pterygo-palatine junction.

2. The postorbital ligament is weak in *Jynx,* fairly strong in other Picidae.

3. The Picinae (but not Jynginae or Picumninae) have a forwardly directed spur from the lateral edge of the auditory capsule, with ligamentous connection (opisthotic ligament) to the quadrate.

4. In *Jynx,* M.a.m.e.rost.temp. is very small; otherwise, M.add.mand.ext. much resembles that of barbets and honeyguides, with M.a.m.e.rost.lat. expanded across M.a.m.e.vent. As in *Indicator*, Ap. 4 is scarcely detectable. In all other Picidae, the muscle is characterized by retention of presumed primitive features, particularly the narrow M.a.m.e.vent., and wide lateral expansion of M.a.m.e.caud.; M.a.m.e.rost.lat. also remains narrow.

5. M.pseud.superf. in *Jynx* has a medial extension of the origin as in barbets and honeyguides. In other Picidae, the muscle has a simple triangular shape, with no medial extension.

6. M.pter.dors.lat. is of normal shape and simple structure in *Jynx*; in other Picidae it is much elongated, and has bipinnate structure.

7. M. protractor is a narrow small muscle in *Jynx,* with no obvious subdivision or attachment to the orbital process of the quadrate. It is greatly enlarged in other Picidae, and consists of two distinct parts. There is extensive attachment on the orbital process, and the region of insertion on the pterygoid is developed as a long bony spur.

8. The tongue is unbarbed in *Jynx,* barbed in other Picidae.

9. Hyoid skeleton and musculature are very similar in all Picidae, including *Jynx*. Their many specialized features include a unique and distinctive muscle, M. geniothyreoideus (perhaps derived from M. geniohyoideus) and a greatly elongated M. hypoglossus obliquus (=M. ceratoglossus superior, Leiber), taking to an extreme the trend seen in other typical Piciformes, especially the Indicatoridae.

10. M. biventer is strongly developed in *Jynx,* weakly in other Picidae.

11. M. longus colli consists entirely of long slips in all Picidae, as also in the Indicatoridae. In *Jynx* (as in honeyguides), these are largely fleshy, but in other Picidae, the insertions of the muscle are made by very strong tendons, fleshy regions being confined to the slips of origin on posterior vertebrae.

It will be clear from this resumé that the central problem in understanding the evolution of the Picidae concerns the origin of the Jynginae. Though endowed with a specialized tongue apparatus very similar to that of woodpeckers, wrynecks totally lack their specializations for excavation, but show a derived condition of M.add.mand.ext. very similar to that of barbets and honeyguides. Obviously, then, either the tongue modifications or those of M.add.mand.ext. arose separately in the Jynginae—or, just conceivably, both. The specialized features of tongue, hyoid and hyoid musculature are numerous, and include the appearance of a muscle (M. geniothyreoideus) apparently unique to the family. On balance, therefore, it seems reasonable to regard the Jynginae as a group which diverged early from woodpecker stock at a stage when tongue modifications had appeared, but not specializations for hammering. If this view is correct, then the structure of M.add.mand.ext. in *Jynx* was derived separately from that in barbets and honeyguides, resemblances being due, perhaps, to similar genetic potential in these groups.

However, the alternative possibility should not be discounted; if wrynecks arose from an early honeyguide/barbet stock, then their jaw muscle similarities would be due to common origin, and the woodpecker-like tongue apparatus must have evolved separately in wrynecks. This is not impossible; the basis for the woodpecker tongue (e.g. long basihyal, very long M. hypoglossus obliquus) already exists in barbets and honeyguides, and only the rather mysterious M. geniothyreoideus would require to be explained. Similarities of palate structure between wrynecks and woodpeckers are probably of minor significance. It would not take much more reduction of ossification in honeyguides to leave vomer and maxillo-palatine vestiges like those of the Picidae; indeed *Prodotiscus* spp. may well prove to have such structure if and when anatomical specimens are ever obtained. It is interesting to note, however, that woodpeckers and piculets clearly went through a wryneck-like phase with reduced skull ossification. Presumably the diet of ants or insect grubs made available by the long tongue places little stress on the skull; hammering, with consequent skull reinforcement, appeared well after adaptations of the tongue as a means of extending the scope for its use.

The present study sheds little helpful light on the origins of the Picumninae, except to make clear that this was well after that of the Jynginae, at a time when all the characteristic woodpecker adaptations had already been acquired. It seems most likely that piculets evolved from some early woodpecker stock to exploit the smaller branches and twigs in tropical habitats, but it scarcely seems possible to single out any group of living woodpeckers as near relatives.

Most functional problems concerning the Picidae have been dealt with at length elsewhere. One aspect perhaps deserving further mention here is the extent of kinetic coupling as against independent jaw action. All the Picidae have a postorbital ligament, though weak in *Jynx*, but they are clearly capable of unloading it to permit a high degree of independent jaw action. Photographs of *Jynx* carrying ants to the nest (e.g. Koffan, 1960) show extreme depression of the upper jaw independent of the lower, and the same is shown in lesser degree by some photographs of woodpeckers, e.g. Burton & Coleman, 1976. Obviously the mechanism of this action and its structural basis require much further study.

Phylogeny and affinities with other orders

To conclude this review, evidence from feeding apparatus structure will be gathered together in an attempt to deduce a possible phylogeny for the Coraciiform—Piciform assemblage. The discussion also briefly considers the origins of the Passeriformes and Trogoniformes and other problems highlighted by the proposals of Feduccia (1977, 1979).

1. Phylogeny

The major division indicated by this study is one between the 'typical Piciformes' (Capitonidae, Indicatoridae, Ramphastidae and Picidae), and the rest (excluding the Bucerotidae, Upupidae and Phoeniculidae, whose position is discussed later). Features in which the two lines differ are numerous and generally consistent, including such major items as the

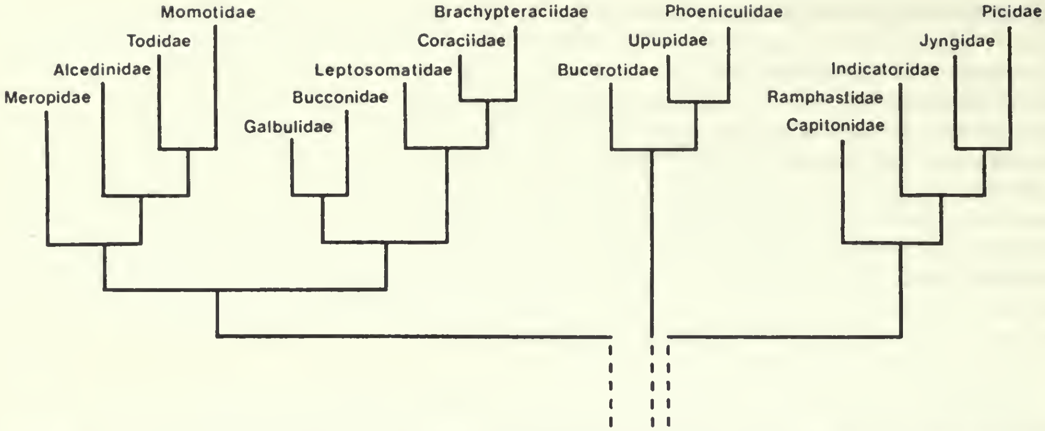

Fig. 32 A possible phylogeny of Coraciiform/Piciform families, as indicated by the features studied here.

structure and siting of M. pseudotemporalis superficialis, form and proportion of the hyoid skeleton, structure of M. hypoglossus obliquus and origin of M. tracheohyoideus. Such differences are fundamental enough to indicate that the two lines have had a long evolutionary separation.

Within the typical Piciformes, the shared characters are predominantly derived ones, and most of them seem unlikely to have arisen more than once. Among the remaining families, the situation is less clear. Those which have been grouped here as 'typical Coraciiformes' share a number of supposedly derived features, such as the invariably desmognathous palate, structure of M. adductor externus and M. pseudotemporalis superficialis, origin of M. branchiomandibularis and M. tracheohyoideus, and largely cartilaginous entoglossum. However, the characters linking them are in some cases less consistent than in the typical Piciformes, and the possibility of some being derived more than once appears stronger. To this group of six families it is necessary to add two more—the Galbulidae and Bucconidae (Galbuloidea). They differ radically from the Piciformes, but agree with the Coraciiformes, in almost all the features which this study has shown to be important. Their closest affinities seem to be with the Coraciidae and Leptosomatidae, and indeed this set of four families (Coraciidae, Leptosomatidae, Bucconidae, Galbulidae) appears from the present study to be a clearer natural group than the remaining Coraciiformes (Alcedinidae, Todidae, Momotidae, Meropidae) though the latter are linked by a derived condition of the stapes (Feduccia 1977, 1979). Significant features of feeding apparatus structure shared by them include the long and stout postorbital process, quadrate with very deep medial condyle and broad orbital process, modification of M. serpihyoideus, and in all but *Leptosomus*, loss of M. stylohyoideus. In the phylogeny, I have consequently grouped them together as a branch diverging early from the main Coraciiform stem.

The remaining three families—the Upupidae, Phoeniculidae and Bucerotidae—also constitute a well defined natural group, sharing such features as a 'retractor palatini' slip of M. pterygoideus, anomalous condition of M. pterygoideus dorsalis, retroarticular process, and reduced hyoid with characteristic hour-glass shaped basihyal. Traditionally, they have long been linked with the Coraciiformes, but on the basis of features analysed here, they appear to occupy an almost exactly midway position between Coraciiform and Piciform stems. Clearly their separation took place early, but there are indications that they had moved some way along the Piciform pathway when this occurred. Persuasive evidence for this view is provided by the structure of M. hypoglossus obliquus, already well modified towards the condition which reaches an extreme in the Picidae. The form and siting of M. pseudotemporalis superficialis is also Piciform rather than Coraciiform. M. tracheohyoideus originates as in the Coraciiform families in the Upupidae and Phoeniculidae, but the existence of an intermediate condition in the Bucerotidae suggests that it may have arrived at this stage independently.

To summarize, then, two main branches are visualized in the phylogeny of this assemblage of families. One, leading to the four families of typical Piciformes, branched at an early stage, giving rise to the Upupidae, Phoeniculidae and Bucerotidae. The other, consisting of the 'typical Coraciiformes', has two branches. One includes the Galbuloidea, together with the Coraciidae, Brachypteraciinae (=Brachypteraciidae) and Leptosomatidae; the other embraces the four diverse remaining families, of which the Todidae and Momotidae are perhaps most closely linked. This phylogeny is depicted in Fig. 26.

2. Morphology of the stapes

Feduccia (1977) produced evidence based on the morphology of the bony stapes which seemed to indicate a diphyletic origin for the Passeriformes, the sub-oscine families seeming to show an affinity with some Coraciiformes (Alcedinidae, Todidae, Momotidae and Meropidae). Further evidence (Feduccia, 1979) compelled him to return to the traditional view that the Passeriformes are a monophyletic group, but his findings could still be interpreted to suggest that the ancestors of the Passeriformes had some affinity with the Coraciiformes.

More interestingly, his 'Alcediniformes', sharing a derived stapedial morphology are equivalent to the suborder Alcedines in the classification proposed here. This clearly reinforces the conclusions of the present study, but at the same time raises a further problem, since the Trogoniformes exhibit the same condition. This small and morphologically uniform group have generally been regarded as a distinct order of uncertain affinities. Feduccia (1977) proposes that they branched off from the same stock as the 'Alcediniformes' (=Alcedines) after these had diverged from the 'Coraciiformes'. I shall shortly undertake detailed study of the trogon feeding apparatus in the hope of clarifying their position, but for the present, a few points perhaps deserve comment.

Firstly, since the Trogoniformes retain well developed basipterygoid processes, these must have been lost independently in Alcediniform and Coraciiform lines; however they have undoubtedly been lost independently by many other bird families, so this factor is clearly no obstacle. Second, and more interestingly, an initial examination of Trogon (*Harpactes*) jaw musculature has revealed that M. pseudotemporalis superficialis is represented by two virtually separate muscles lying side by side. In structure and siting, the medial part corresponds remarkably closely with the deeper, medial M. pseud. superf. of the Piciformes, while the lateral one corresponds with the more lateral and superficial muscle of the typical Coraciiformes. The presence of both at once appears to be the ancestral condition in an almost idealized form. If Feduccia's phylogeny is correct, then here again, the same derived condition—loss of the medial muscle—has arisen independently in both 'Alcediniformes' and 'Coraciiformes'. Thirdly, Trogons lack any trace of desmognathism; consequently, this condition too, must have arisen independently in 'Alcediniformes' and 'Coraciiformes'. A final point concerns the 'retractor palatini' slip of M. pterygoideus—a slip from the muscle attached to the basitemporal plate. Among the families studied in this investigation, this feature is found only in the Bucerotidae, Upupidae and Phoeniculidae. However, a 'retractor palatini' is also found in Trogons (Burton, 1974), as in many passerines, but it appears to be of different morphological origin; it is therefore probably of little relevance as regards their phylogenetic placing.

Finally, some comment on the hornbills, hoopoes and wood hoopoes. Feduccia finds that the latter two families share a unique 'anvil' modification of the stapes, whereas the hornbills retain the primitive condition. This is consistent with the findings of the present study inasmuch as the hoopoes and wood hoopoes are shown to be particularly closely related, but I am reluctant to follow him in placing them in a separate order from the hornbills. This investigation has added to the already strong evidence that the three families constitute a distinct natural group, and the classification should reflect this, as in the scheme which follows.

3. Classification

A suggested classification of the Coraciiform and Piciform families is given below; it is based solely on the results of this study, as expressed in the postulated phylogeny depicted in Fig. 26. Ground rollers have been elevated to family status following Cracraft (1971) and wrynecks are given family status for reasons explained earlier in this systematic review. The Capitonidae and Ramphastidae are retained as separate families, though it may be noted that in a strictly cladistic system, their relationship as viewed here (pp. 433–4) should be expressed by merging them as a single family. (See, e.g. Cracraft, 1974). Only extant groups are included in this classification, but hopefully it may eventually prove possible to include fossil discoveries (e.g. Brodkorb, 1976, Feduccia & Martin, 1976, Olson, 1976) within a similar framework.

It would of course be gratifying if future studies of these families from other aspects produce similar results to those presented here, but doubtless some inconsistencies will occur. Where this is the case, I can only hope that the findings of this study have been presented clearly enough to make reinterpretation or reworking feasible.

The proposed classification, then, is as follows:

Order **CORACIIFORMES**

- Suborder ALCEDINES
    - Family Meropidae, bee-eaters
    - Family Alcedinidae, kingfishers
    - Family Todidae, todies
    - Family Momotidae, motmots
- Suborder CORACII
    - Superfamily Galbuloidea
        - Family Galbulidae, jacamars
        - Family Bucconidae, puffbirds
    - Superfamily Coracoidea
        - Family Leptosomatidae, cuckoo-rollers
        - Family Coraciidae, rollers
        - Family Brachypteraciidae, ground-rollers

Order **UPUPIFORMES**

- Superfamily Bucerotidea
    - Family Bucerotidae, hornbills
- Superfamily Upupoidea
    - Family Upupidae, hoopoes
    - Family Phoeniculidae, wood-hoopoes

Order **PICIFORMES**

- Family Capitonidae, barbets
- Family Ramphastidae, toucans
- Family Indicatoridae, honeyguides
- Family Jyngidae, wrynecks
- Family Picidae, woodpeckers

Acknowledgements

No anatomical study can take place without specimens. At the onset of this project, although the collections of the British Museum (Natural History) could provide a large part of the requirements, various crucial species or groups still remained unrepresented. Most of these gaps have now been filled, partly by direct collecting, and partly by gifts, exchanges or loans. Outstanding among the gifts are the valuable specimens presented by Con Benson, Hilary Fry, Bill Peckover, Alan Phillips and Amadeo Rea. I am grateful to Dean Amadon and later Wesley Lanyon for loaning various specimens in the care of the American Museum of Natural History, and to M. Louette of the Musé Royal de l'Afrique Centrale, Tervuren for allowing me to examine a specimen of *Prodotiscus*. Gerlof Mees kindly allowed me to examine skeletons in the Rijksmuseum van Natuurlijke Historie, Leiden.

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Dr Ethelwynn Trewavas

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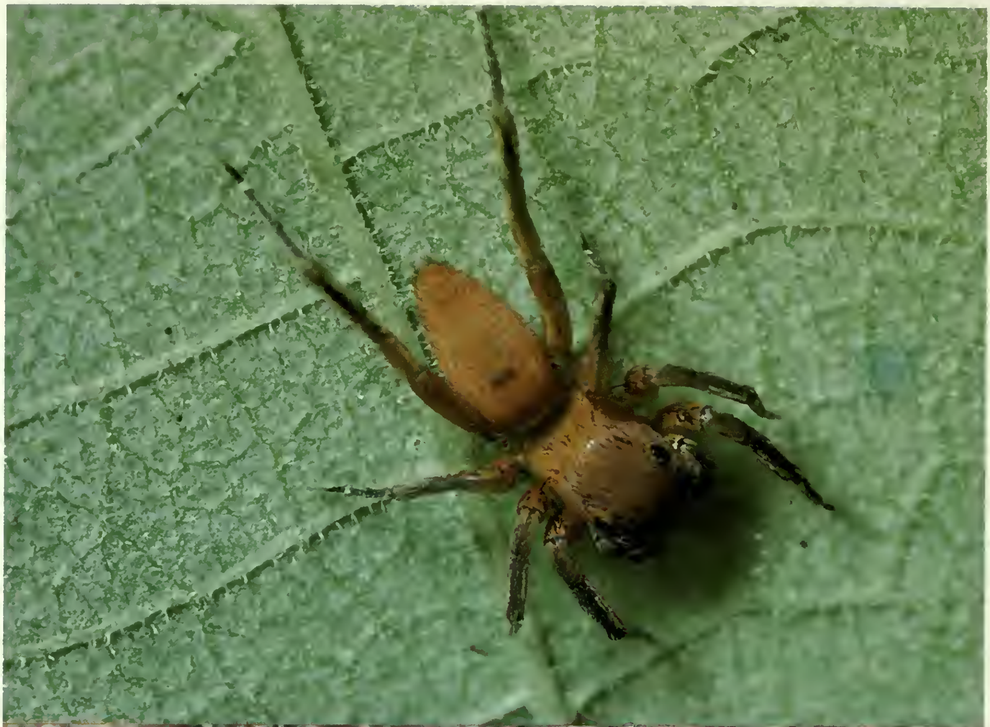

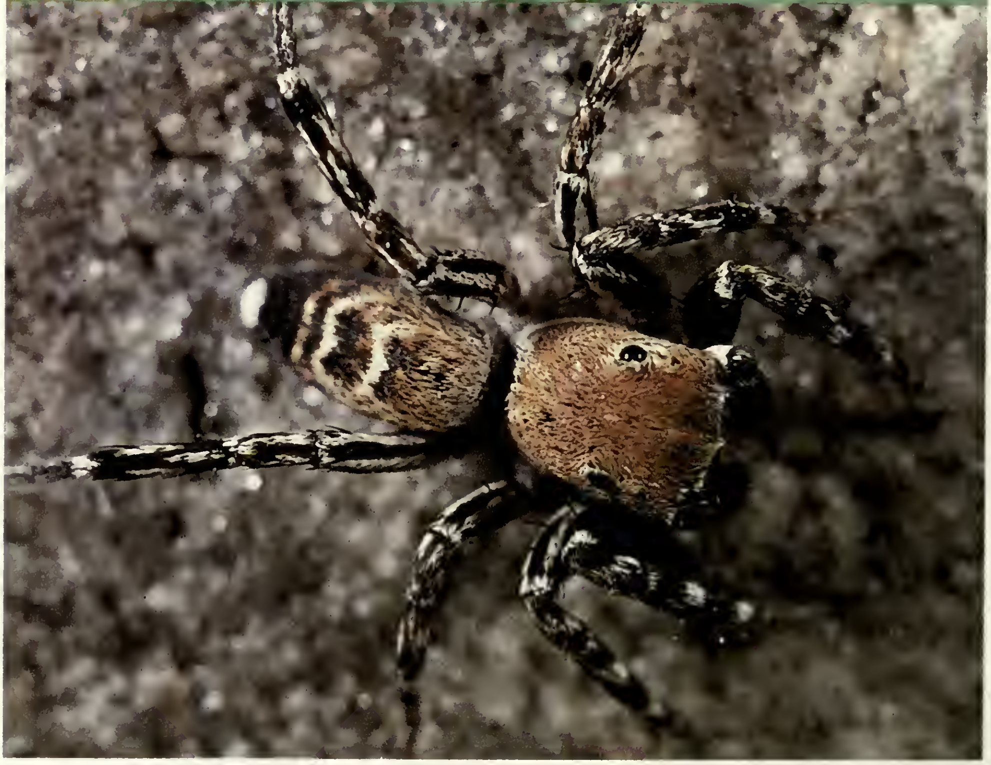

Fig. 1 (above) *Cyrba bimaculata* Simon, ♂ from Kenya; mytiliform field conspicuous as a greyish patch on the abdomen. **Fig. 2** (below) *Cyrba algerina* (Lucas), from Majorca; mytiliform field inconspicuous.

A revision of the spider genus *Cyrba* (Araneae: Salticidae) with the description of a new presumptive pheromone dispersing organ

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Introduction

Cyrba Simon, 1879 is a small old world genus comprised of seven species presently classified in the Spartaeinae (Wanless, 1984) and the present work completes a preliminary revision of the entire subfamily. Four additional taxa originally described in *Cyrba,* two of which are described below, are treated here as *species incertae sedis* and have not been taken into account when defining or discussing any characters of the genus.

The species comprising *Cyrba* seem to form a good monophyletic group, which however, cannot as yet be clearly defined by uniquely derived characters. The form of the bilobed caudal plate of the epigyne represents a possible synapomorphy, but for the present the genus is supported by a combination of characters which together separate *Cyrba* from other spartaeine genera (see below). The genus is best known from *C. algerina* (Lucas) a brightly coloured species frequently found under stones throughout the Mediterranean Region. Yet, in spite of an extensive bibliography (Bonnet, 1956), little is known of the biology of that species; studies on the mating behaviour of *C. algerina* (Legendre & Llinares, 1970) representing virtually all that can be found on *Cyrba* behaviour (Jackson, pers. comm.). Fortunately, through the courtesy of Mr and Mrs J. Murphy, London and Mr P. D. Hillyard, BM(NH), it was possible to send live continental specimens of *C. algerina* to Dr R. R. Jackson, University of Canterbury, New Zealand who will report on his studies in a separate paper.

Wanless (1984) suggested that on the basis of certain behavioural and morphological characters the subfamily Spartaeinae belonged in one of the most primitive branches of the Salticidae. Thus, the pervasive use of webs by *Portia* (Jackson & Blest, 1982) and presence of large posterior median eyes in most spartaeine genera (see also Blest, 1983) were considered to be primitive characters which have been lost by the advanced salticids. The occurrence of secretory organs on the femora of legs I in adult males which are arguably producing sex pheromones (Wanless, 1984) and behavioural evidence of pheromonal detection in *Cyrba* (Legendre & Llinares, 1970; Jackson, in press), *Brettus* Thorell and *Portia* (Jackson, in press) gives further support to the 'primitive' hypothesis, since pheromonal activity might reasonably be viewed as a primitive trait in a group of animals which are invariably described as predators almost wholly dependent on vision. The discovery in certain spartaeine genera and in *Holcolaetis* Simon (a member of the *Cocalodes*-group, sensu Wanless, 1984) of abdominal 'secretory' organs which are possibly associated with the dispersal of pheromones is of special interest. In both groups they occur in subadults and adults of both sexes, but their structure and assumed mode of function is markedly different.

Abdominal 'secretory' organs

Fields or patches of abdominal 'secetory' organs (Fig. 3A, B) are only known to occur in certain groups of 'primitive' salticids (see below). At low magnifications they are usually obscure and easily overlooked, but when evident especially in freshly preserved or living

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spiders they sometimes appear as a greyish patch situated on the dorsum of the abdomen, between or immediately in front of the anterior apodemes (Figs 1; 5A, D). The patch is normally surrounded by abdominal setae (Figs 16A, B; 17A, C) and when examined in fresh material is often seen to contain minute lightly sclerotised spots (the individual 'secretory' organs) and a few scattered microsetae. SEM studies have shown that there are evidently two basic types of 'secretory' organ, i.e. mytiliform in the Spartaeinae and pustuliform in *Holcolaetis,* a member of the *Cocalodes*-group (Fig. 3A, B).

Mytiliform fields are comprised of 35 to 50 irregularly spaced mytiliform organs which are usually characterised by their resemblance to a mussel shell valve. Examples of mytiliform organs from *Cyrba, Portia* and *Gelotia* Thorell are given in Figs 16A–F; 17A–F; 18A–F; 19A–F. The mytiliform profile is for the most part retained in *Cyrba* and *Portia,* but is less evident in *G. syringopalpis* Wanless (Fig. 18D–F). Unfortunately the full extent and development of mytiliform fields within spartaeine groups has not been fully established for they are difficult to detect in bleached or rubbed specimens and it has not been possible to examine every species concerned. Nevertheless mytiliform fields undoubtedly occur in the following:

(a) *Cyrba*: both sexes of all species; subadults of *C. algerina.*
(b) *Portia*: all males, excluding *P. albimana* (Simon); all females; subadults of *P. labiata* (Thorell) and juveniles of *P. fimbriata* (ca. instars 3 to 5).
(c) *Gelotia syringopalpis*: males and females.
(d) *Cocalus* sp. undescribed female, not examined by SEM.
(e) *Mintonia* sp. undescribed female, not examined by SEM.

Pustuliform fields are relatively more extensive and are each comprised of about 160 closely spaced pustuliform organs (Figs 3B; 20A, B) which differ from mytiliform organs in shape and by having the margins of each pustule surrounded by a thick rim of cuticular pleating (Fig. 20C). They occur in most species of *Holcolaetis* Simon and in subadult females of *H. vellerea* Simon, but are evidently lacking in other genera of the *Cocalodes*-group.

The presence of relatively large pores in both types of organ suggests that they are either secretory or sensory in function and that they may be homologous with slit sensilla (strain or stress receptors), which also appear to possess minute pores. These pores are, however, the attachment sites of dendrites (Foelix, 1983) and do not seem to correspond with the pores found in abdominal 'secretory' organs. Furthermore, the majority of slit sensilla occur on the legs in areas of particular mechanical stress or 'interest' (Barth in Witt & Rovner, 1982), whereas the abdominal 'secretory' fields occur in soft cuticle away from areas of stress; homology with slit sense organs is therefore unlikely. In spartaeine genera the shape of the organs, the occasional presence of shallow gullies (Figs 18E; 21B) and the presence of an amorphous substance in two specimens (Fig. 19B, E) appears to indicate that a secretion is produced, possibly a pheromone which fills the bowl of the mytiliform organ to evaporate slowly. Pustuliform organs could function in a similar manner and produce a secretion which collects around the margins of the pustule. However, it is possible that spherical bodies found in association with the organs (one specimen) and lodged in their pores (Fig. 20A–E) have been secreted by them, for their diameters (*ca.* 1·3 µm) correspond closely with one another—unlike that of certain fungal contaminants referred to below. The spheres are apparently covered in minute pits or pores which are unfortunately difficult to resolve as they become distorted at high SEM magnifications (Fig. 20F); evidence of clumping (Fig. 20B) suggests that they may well possess adhesive properties. The purpose of the spheres, if any, is of course unknown, but it is not inconceivable that they evaporate and are in themselves pheromones or alternatively packets that slowly release pheromones through surface pores.

Although the present study clearly favours a secretory function the entire hypothesis could be based on a set of artifacts, the secretions and spheres may be contaminants as none of the specimens were cleaned prior to examination by SEM. They may also have arisen as

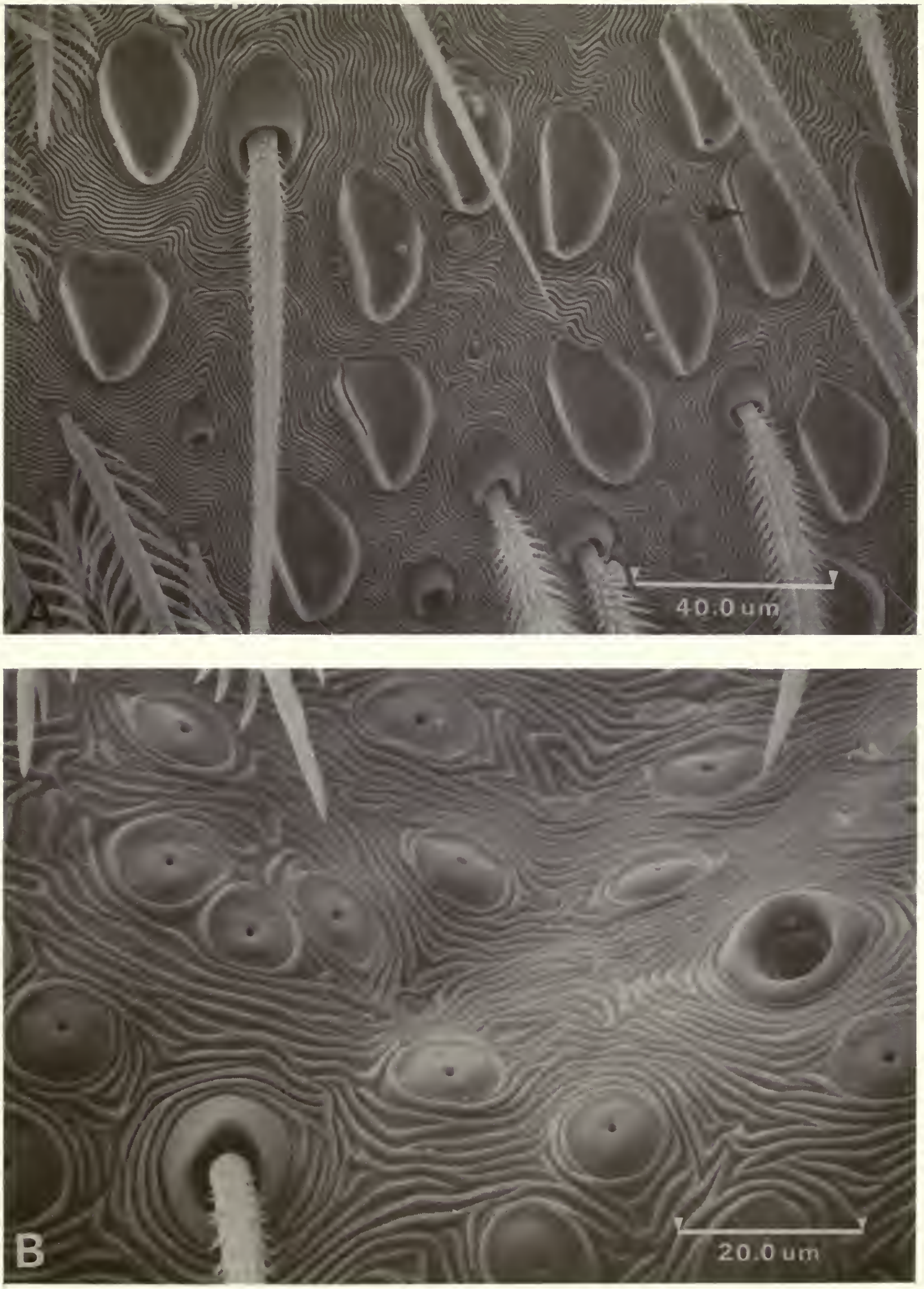

Fig. 3 A, *Portia labiata* Thorell, ♂, mytiliform field, ×730. B, *Holcolaetis vidua* Lessert, subadult ♀, pustuliform field, ×1350.

a result of coagulation in 75% alcohol, a fixative routinely used for both killing and preserving spiders. In fact there is evidence of fungal contamination in one specimen of *P. labiata* (Fig. 21A–E) which at first sight seems to possess a scattering of spheres similar to those found in *Holcolaetis.* The bodies, however, are reminiscent of conidia seen in some species of *Penicillium* and *Aspergillus* (Dr A. H. S. Onions, pers. comm.) which could have infected the specimen in life or while it was being prepared for SEM.

The presence of abdominal 'secretory' organs, which have conceivably evolved from pores or setal sockets, could provide a useful synapomorphy linking both Spartaeinae and the *Cocalodes*-group, since the latter, as suggested by Wanless (1984), probably merits subfamilial rank. However, the proposal is possibly unsound as Kullman & Stern (1975) have illustrated an isolated pustuliform organ in the abdominal cuticle of the water spider *Argyroneta aquatica* (Clerck) (Family Argyronetidae) which is indistinguishable from and probably homologous with those of *Holcolaetis.* Isolated organs and even 'secretory' fields may therefore occur in other spider families.

Preliminary experiments performed by Dr R. R. Jackson implicate *Portia* mytiliform structures as pheromone sources. If this is confirmed and current histological studies by Professor R. Legendre and Dr A. Lopez reveal the presence of exocrine glands in the integument, a more appropriate name for these organs can be proposed. Although care will be needed since the function of these fields is possibly more complex than has been suggested, for the microsetae referred to above possess minute basal openings, paired in *Holcolaetis* (Fig. 22B, D, F), single in *Cyrba* (Fig. 22E) and *Portia* (Fig. 22C). The raised rim of the openings (Fig. 22C) bear a superficial resemblance to those found in slit sensilla (Foelix, 1982) so presumably, they too could be sites of dendrite attachment and thus sensory in function.

It is perhaps worth noting that the practice of marking the abdomens of live spiders with fluorescent paint, to facilitate the identification of individuals in field experiments is not to be recommended, at least in so far as this group of salticids is concerned.

Genus ***CYRBA*** Simon

Salticus [in part]: Lucas, 1846: 136. Pickard-Cambridge, O. 1872: 321.

Attus [in part]: Koch, 1867: 874, 876. Simon, 1868: 24, 547, 550; 1871: 219.

Euophrys [in part]: Kroneberg, 1875: 48. Pavesi, 1878: 392.

Cyrba Simon, 1876: 165. Type species *Salticus algerina* Lucas, by original designation. Simon, 1901: 387, 429, 447, 449 [=*Stasippus*]; 1937: 1146, 1245. Scudder, 1882: 89. Peckham & Peckham, 1886: 269, 318; 1888: 8. Marx, 1890: 574. Kulczyński, 1890: 15. Chyzer & Kulczyński, 1891: 3, 38. Planet, 1905: 271. Franganillo Balboa, 1917: 201. Petrunkevitch, 1928: 186. Berland, 1929: 68, 70. Gerhardt & Kästner, 1938: 636. Neave, 1939, I: 945. Roewer, 1954: 984. Bonnet, 1956: 1337. Prószyński, 1976: 17. Hubert, 1979: 229, 233. Wanless, 1984.

Stasippus Thorell, 1887: 374. Type species *Stasippus inornatus* Thorell, by original designation and monotypy. Petrunkevitch, 1928: 247. Neave 1940, IV: 275.

Vindima Thorell, 1895: 348. Type species *Vindima maculata* Thorell, by original designation and monotypy. Waterhouse, 1902: 392. Petrunkevitch, 1928: 251. Neave, 1940, IV: 641. Roewer, 1954: 1703. Bonnet, 1955: 768; 1959: 4797.

Astia [in part]: Simon, 1901: 436.

DEFINITION. Spiders of medium size, i.e. between 4·0 and 8·0 mm long. Sexual dimorphism sometimes evident in colour markings and development of legs I which are slightly enlarged in females. Species often brightly coloured. Males, females and subadults with a usually indistinct mytiliform field situated just anterior to the first pair of abdominal apodemes.

Carapace: longer than broad, of medium height and widest about level between coxae II–III; fovea long and sulciform, apex positioned just behind posterior margins of posterior lateral eyes. *Eyes*: with moderately pronounced lenses set on low tubercles; laterals with black surrounds; anteriors subcontiguous with apices more or less level or slightly recurved in frontal view; anterior laterals greater than half diameter of anterior medians; posterior medians relatively small, positioned closer to posterior laterals and just outside optical axis of anterior laterals; posterior laterals about as large as anterior laterals and set inside lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle occupying between 42 and 53% of carapace length. *Clypeus*: between 27–48% diameter of anterior median eyes in males and 10–16% in females. *Chelicerae*: generally vertical and parallel, of medium size, but slightly more robust in female; fang moderately strong; promargin with three teeth, retromargin with three to five. *Maxillae*: of medium length, more or less parallel with rounded apices. *Labium*: slightly longer than broad, about half maxillae length. *Sternum*: generally elongate scutiform. *Pedicel*: short. *Abdomen*: usually elongate ovoid with an obscure mytiliform field; patterns sometimes distinctive especially in living or freshly preserved specimens; spinnerets moderately long and more or less subequal in length, anteriors robust, medians slender, posteriors moderately robust; anal tubercle cone-shaped, sometimes strikingly white haired; position of colulus indicated by scanty group of setae between tracheal slit and base of spinnerets; tracheal slit obscure, positioned just anterior to anterior spinnerets. *Legs*: moderately long

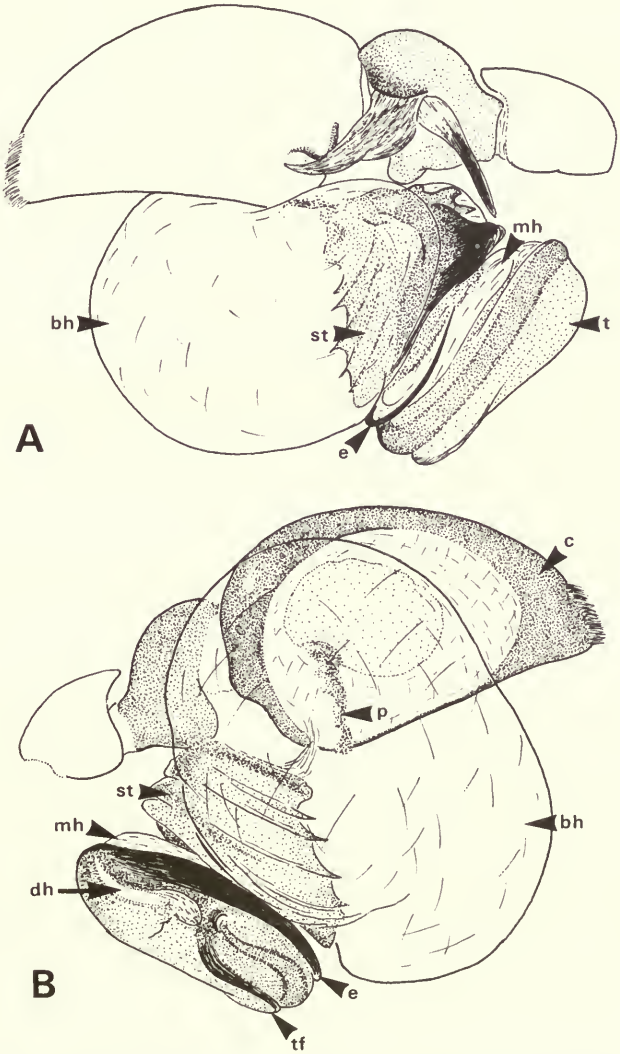

Fig. 4 *Cyrba algerina* (Lucas), expanded ♂ palp: A, retrolateral; B, prolateral. Abbreviations: bh, basal haematodocha; c, cymbium; dh, distal haematodocha; e, embolus; mh, median haematodocha; p, petiole of basal haematodocha; st, subtegulum; t, tegulum; tf, tegular furrow.

and slender; tibiae and patellae of front pairs slightly dilated in females; claws usually pectinate; tufts present, scopulae absent, but rows of minute shining setae present on underside of tarsi and metatarsi; spines moderately strong and numerous, but fewer spines on legs I–II in females; basic spination of legs I variable in males, more stable in females—usually metatarsi v 2-0-0, tibiae v 2-2-2, femora d 0-2-2, p 0-0-1. *Female palps*: moderately long with an apical claw, distal segments usually darker than proximal ones. *Epigynes*: Intergenerically fairly distinct, but sometimes similar interspecifically; characterised by a usually bilobed caudal ledge bearing crescent-shaped embolic guides (Fig. 6D) uniting medially and extending anteriorly to fuse with the introductory ducts and form indistinct copulatory openings; lateral slits in epigynal area (Fig. 12E) or pouches in caudal ledge (Fig. 13G, H) rarely present; introductory ducts moderately long, proximally contiguous, but distally separate and curving (see remarks below); spermathecae large, dark and usually rounded bearing leaf-like fertilisation ducts on posterior margin (Fig. 6E, arrowed). *Male palps*: Interspecifically and intergenerically fairly distinct. Complex with variously developed protuberances on anterodorsal margins of patellae, tibiae and basal retrolateral margin of cymbium; femora moderately long; patellae with pronounced anterodorsal protuberance (Fig. 8A, arrowed), retrolateral flange (Fig. 11B, arrowed) rarely present; tibiae with an oblique ventral apophysis and retrolateral apophyses of various forms—simple with hyaline elements, fan-like or with an accessory prong; cymbium with distal scopula and characteristic process on retrolateral basal margin (Fig. 8A, arrowed), also a less conspicuous basal depression opposite the anterodorsal protuberance of the patellae; embolus long, slender and curving, sometimes with a conspicuous basal prong; distal haematodocha evident as a narrow membraneous stripe (Fig. 9E, arrowed) giving rise to a delicate petal-like lobe (M_1 of Wanless, 1984); tegulum rounded to subovoid with peripheral seminal duct becoming sinuous distally, an open tegular furrow bearing along its outer wall and embolic guide or groove (Fig. 10F, arrowed) and an indistinct tegular ledge (Fig. 11C, arrowed; M_3 of Wanless, 1984); median haematodocha small and tube-like in expanded palp; subtegulum cone-shaped with pronounced spiral ledges; basal haematodocha bulbous in expanded palp with petiole arising from basal retrolateral margin of alveolus (Fig. 4B).

REMARKS. (a) Expanded palps have only been examined in *C. algerina*. (b) The precise nature of the introductory ducts is difficult to determine for the distal elements are folded and appear to have fused, one-above the other (Fig. 6C) with the presence in some species of additional lobe-like folds (Figs 8F; 9I, arrowed), which appear as dark patches in uncleared epigynes (Fig. 8E, arrowed).

DIAGNOSIS. *Cyrba* may be distinguished from most genera in the subfamily Spartaeinae by the combined presence of an elongate fovea and small posterior median eyes. The only area where difficulties may arise is with three species of *Gelotia* (*G. argenteolimbata* Simon *G. bimaculata* Thorell and *G. frenata* Thorell) which also possess small posterior median eyes and a moderately long fovea. Confusion, however, is rather unlikely as the secondary genitalia of *Gelotia* species are quite distinct from those of *Cyrba*—males of *Gelotia* possess a cap-like retrolateral tibial apophysis, whereas the epigynes are characterised, at least in the species concerned, by a median ridge (Wanless, 1984).

AFFINITIES. Wanless (1984) suggested that on the basis of palpal morphology the genera *Cyrba, Brettus* Thorell, *Neobrettus* Wanless, *Phaeacius* Simon and *Portia* appeared to form a natural group within the Spartaeinae. *Cyrba* was associated with *Brettus* and *Neobrettus* while at the same time showing some affinities with *Portia. Portia* however, was tentatively linked with *Phaeacius,* a proposal which should now be reviewed as recent studies (Jackson, in press) have shown that *Phaeacius* species are flattened sit-and-wait predators behaviourally quite different from tested species of *Cyrba, Brettus* and *Portia,* which are rapidly moving cursorial predators of insects and specialised web-invading predators of other spiders. If the palpal organs of *Phaeacius* are also taken into account, then the presence of several unique characters (Wanless, 1984) would seem to confirm its somewhat isolated position, and although an undoubted member of the group it is probably not as close to *Portia* as originally supposed. In fact the closest relative of *Portia* would now seem to be *Cyrba*, for the structure of the epigyne, especially the development of the embolic guides in relation to the openings of the introductory ducts (Fig. 6B, D) and presence of the palpal cymbial flange (Fig. 6A, arrowed), both possible synapomorphies, together with other palpal similarities noticed by Prószyński (1978) support a *Cyrba/Portia* dichotomy in spite of marked differences in habitus and development of palpal retrolateral tibial apophyses.

Check list, known sex and distribution of species of *Cyrba*

Cyrba algerina (Lucas, 1846)	♂♀	Canary Islands; Guinea Bissau; India, Himalayas; Mediterranean Region; USSR, Tadjikistan.
C. bimaculata Simon, 1886	♂♀	Angola; Burundi; Cameroon; Kenya; Nigeria; Zaire
C. boveyi Lessert, 1933	♂♀	Angola; Kenya; Mozambique
C. legendrei sp. n.	♂♀	Comoro Islands; Madagascar
C. lineata sp. n.	♀	South Africa
C. nigrimana Simon, 1900	♀	South Africa
C. ocellata (Kroneberg, 1875)	♂♀	Australia, Wilson Island; Bhutan; Burma; French Somaliland; India; Java; Kenya; Nepal; Philippines; Singapore; Sri Lanka; Thailand; USSR, Tadjikistan; Vietnam.
Species Incertae Sedis		
Cyrba armillata Peckham & Peckham, 1907	♂♀	Borneo
C. bidentata Strand, 1906	♀	Ethiopia
C. dotata Peckham & Peckham, 1903	♀	South Africa
C. szechenyii Karsch in Lendl, 1897	♀	Hong Kong

Key to species of *Cyrba*

Males (those of *lineata* and *nigrimana* unknown)

1 Embolus with pronounced basal prong (Figs 10F; 11C) 2
Embolus without basal prong 3
2 Retrolateral tibial apophysis large and fan-like (Fig. 11C) Angola, Kenya, Mozambique ***C. boveyi*** Lessert (p. 463)
– Retrolateral tibial apophysis a slender prong (Fig. 10I) Angola, Burundi, Cameroon, Kenya, Nigeria, Zaire . . . . ***C. bimaculata*** Simon (p. 461)
3 Retrolateral tibial apophysis with accessory blade-like prong (Fig. 5C, I) Canary Isl., Guinea Bissau, Mediterranean Region, Tadjikistan, Indian Himalayas . . . . . ***C. algerina*** (Lucas) (p. 452)
– Retrolateral tibial apophysis without an accessory blade-like prong 4
4 Basal spur of retrolateral tibial apophysis relatively large and supported by a small angular ledge (Fig. 9D, arrowed) Comoro Isl., Madagascar . . ***C. legendrei*** sp. n. (p. 458)
– Basal process of retrolateral tibial apophysis relatively small, angular ledge absent (Fig. 8A, B) Ethiopian and Oriental regions . . . . ***C. ocellata*** (Kroneberg) (p. 455)

Females

1 Epigynal area with darkened lateral slits (Fig. 12E, arrowed) South Africa . . . . . ***C. nigrimana*** Simon (p. 465)
– Epigynal area without lateral slits 2
2 Epigynal caudal ledge with transverse suture (Fig. 11D, arrowed) Central and Southern Africa . . . . ***C. boveyi*** Lessert (p. 463)
– Epigynal caudal ledge without transverse suture 3
3 Epigynal caudal ledge with large lateral pouches (Fig. 13G, H, arrowed) and relatively acute posterior lobes (Fig. 13F, arrowed) South Africa . . . . ***C. lineata*** sp. n. (p. 465)

– Epigynal caudal ledge without lateral pouches and more or less obtuse posterior lobes . 4

4 Epigynal area hardly if at all wrinkled; lobe of introductory ducts always present (Figs 8E–F; 9H, I: 10J, K) and sometimes visible as a dark patch in uncleared epigynes . 5

– Epigynal area wrinkled; lobes of introductory ducts never present (Fig. 6B, D) Canary Isl., Guinea Bissau, Mediterranian Region, Tadjikistan, Indian Himalayas . . . . ***C. algerina*** (Lucas) (p. 452)

5 Epigynal caudal ledge with anterior margin of embolic guides extending laterally (Fig. 8C–E, arrowed) Ethiopian and Oriental Regions . . . ***C. ocellata*** (Kroneberg) (p. 455)

– Epigynal caudal ledge with anterior margins of embolic guide extending anteriorly (Figs 9H, 10J, K, arrowed) 6

6 Epigynal caudal ledge relatively broad with deep median notch and large lobes (Fig. 10J) Angola, Cameroon, Kenya, Nigeria . . . . ***C. bimaculata*** Simon (p. 461)

– Epigynal caudal ledge relatively narrow with shallow median notch and slight lobes (Fig. 9H) Comoro Isl., Madagascar . . . . ***C. legendrei*** sp. n. (p. 458)

Cyrba algerina (Lucas)

(Figs 2; 4A, B; 5A–I; 6A–E; 16A–F; 17A–D)

Salticus algerinus Lucas, 1846: 148, ♂, ♀. [types not examined ? lost].

Attus leporinus Koch, 1867: 874, ♀. [type not examined, ? lost].

Attus armiger Koch, 1867: 876, ♂. [type not examined, ? lost].

Attus diversipes Simon, 1868: 550, ♀. [type not examined, ? lost].

Salticus cephalotes (Sim.): O.P.-Cambridge, 1872: 321. [presumably lapsus calami for *Salaticus algerinus* Lucas].

Cyrba algerina: Simon, 1876: 167, [=*leporinus*, =*armiger*, =*diversipes*, =*cephalotes*]. Thorell, 1890: 83. Roewer, 1954: 984. Bonnet, 1956: 1338. Andreeva, 1969: 90. Prószyński, 1971: 396; 1978: 18. Schmidt, 1973: 348; 1975: 513; 1976: 315; 1977: 66. Hubert, 1979: 233. Wanless, 1984.

REMARKS. 1. The lost types referred to above have possibly been destroyed or as seems more likely mixed with more recent collections of *C. algerina*, in any event they cannot be found. Since *C. algerina* is the type species of *Cyrba* a female from Algeria is designated neotype. Other neotype designations are however, hardly necessary as the synonymy proposed by Simon (1876) is accepted.

2. A complete bibliography for *C. algerina* may be found in the catalogues of Roewer (1954) and Bonnet (1956).

DIAGNOSIS. Males of *C. algerina* are easily recognised by the form of the retrolateral tibial apophysis (Fig. 5C). Females are more difficult as the epigyne, which may have to be cleared in lactic acid, closely resembles those of *C. bimaculata, C. ocellata* and *C. legendrei.* Female *algerina* however, differ by having a noticeably wrinkled epigynal area (Fig. 6D) and by the absence of lobe-like folds at the distal ends of the curved portions of the introductory ducts (Fig. 6B, arrowed).

MALE from Crete, in good condition. *Carapace* (Fig. 5B, D): light orange with blackish quadrangle and margins; clothed in recumbent pale orange hairs with some whitish ones on lower slopes of thoracic part. *Eyes*: with black surrounds, fringed by orange and whitish hairs with scattered bristles above anteriors and below laterals. *Clypeus*: orange suffused black; thinly clothed in stout black hairs with scanty vertical stripes of white hairs centrally and at level of outer edges of anterior median eyes. *Chelicerae*: dull orange with median black markings; clothed in scattered black hairs with few whitish ones basally; promargin with three teeth, retromargin with four. *Maxillae and labium*: yellow-brown faintly tinged black with paler tips. *Sternum*: dull orange suffused with some black, shiny, thinly clothed in stiff brown-black hairs and vague whitish ones. *Coxae*: yellow-brown faintly tinged black, shiny, thinly clothed in fine black and white hairs. *Abdomen*: dull orange-brown suffused and mottled with some black; clothed in black lanceolate hairs and some bristles with conspicuous dorsal markings comprised of whitish and snow-white hairs; venter also black, but with thin longitudinal stripes on either side; mytiliform field obscure; spinnerets black with greyish tips. *Legs*: legs I tarsi yellow-brown, other segments orange-brown heavily suffused black especially tibiae; remaining legs generally orange-brown with black marks and streaks; clothed in black and white hairs forming more or less distinct patches on tibiae and patellae of legs II and longitudinal stripes on dorsum and sides of

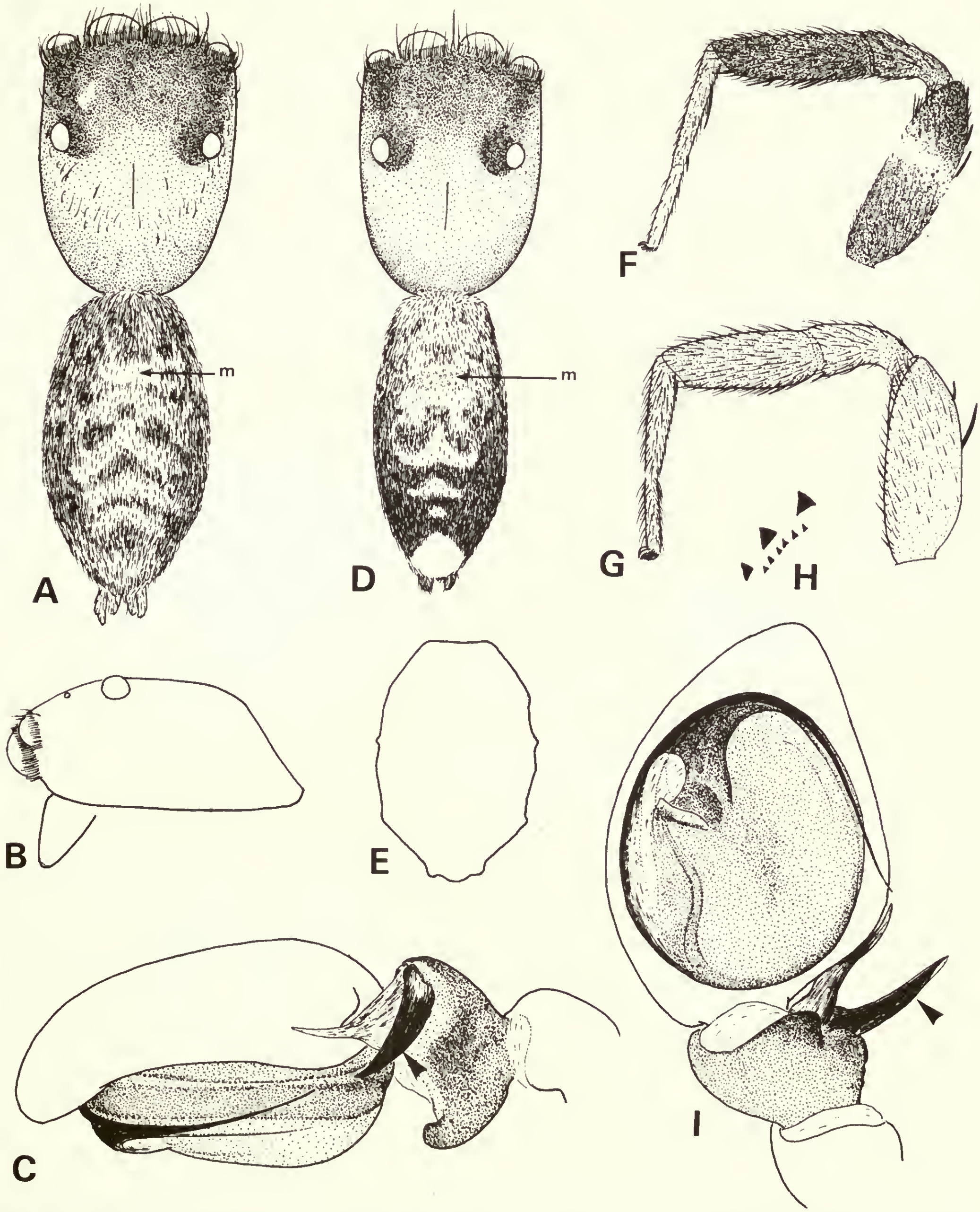

Fig. 5 *Cyrba algerina* (Lucas). ♀: A, dorsal; E, sternum; G, leg I; H, cheliceral teeth. ♂: B, carapace, lateral; C, palp retrolateral; D, dorsal; F, leg I; I, palp, ventral. Abbreviation: m, mytiliform field.

femora. Spination of legs I: metatarsi v 2-0-1, p 0-1-0, r 0-1-1, d 0-0-2; tibia v 2-2-2, p 1-0-1, r 1-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-2, p 0-0-1. *Palp* (Figs 5C, I; 6A): femur and patella yellow-brown suffused with some black, tibia and cymbium heavily suffused black, the latter with an iridescent sheen.

Dimensions (mm): total length 4·6; carapace length 2·18, breadth 1·52, height 1·07; abdomen length 2·4; eyes, anterior row 1·5, middle row 1·24, posterior row 1·32; quadrangle length 1·04 (47% of carapace length). *Ratios*: AM : AL : PM : PL :: 11·5 : 7 : 1·2 : 6·4; AL–PM–PL :: 9–6; AM : CL: :: 11·5 : 3·5.

FEMALE from Crete, in good condition, *Carapace* (Fig. 5A): light orange with blackish quadrangle and sooty margins; clothed in whitish/grey hairs and scattered bristles. *Eyes*: with black surrounds; fringed by buff hairs. *Clypeus*: orange suffused black, thinly clothed in rather strong long black hairs. *Chelicerae*: light orange tinged with some black; clothed in scattered black hairs and a few whitish ones basally; promargin with three teeth, retromargin with six. *Maxillae and labium*: orange-brown faintly tinged black with whitish tips. *Sternum and coxae*: pale orange-brown, shiny and thinly clothed in stiff brown-black hairs. *Abdomen*: yellow-brown suffused and mottled with some black; dorsally clothed in scattered bristles with golden and black lanceolate hairs forming a vague pattern of spots and chevrons; venter clothed in fine black and greyish hairs, mytiliform field obscure; spinnerets whitish with anteriors and posteriors suffused black. *Legs* (Fig. 5G): orange-brown except tibiae I which

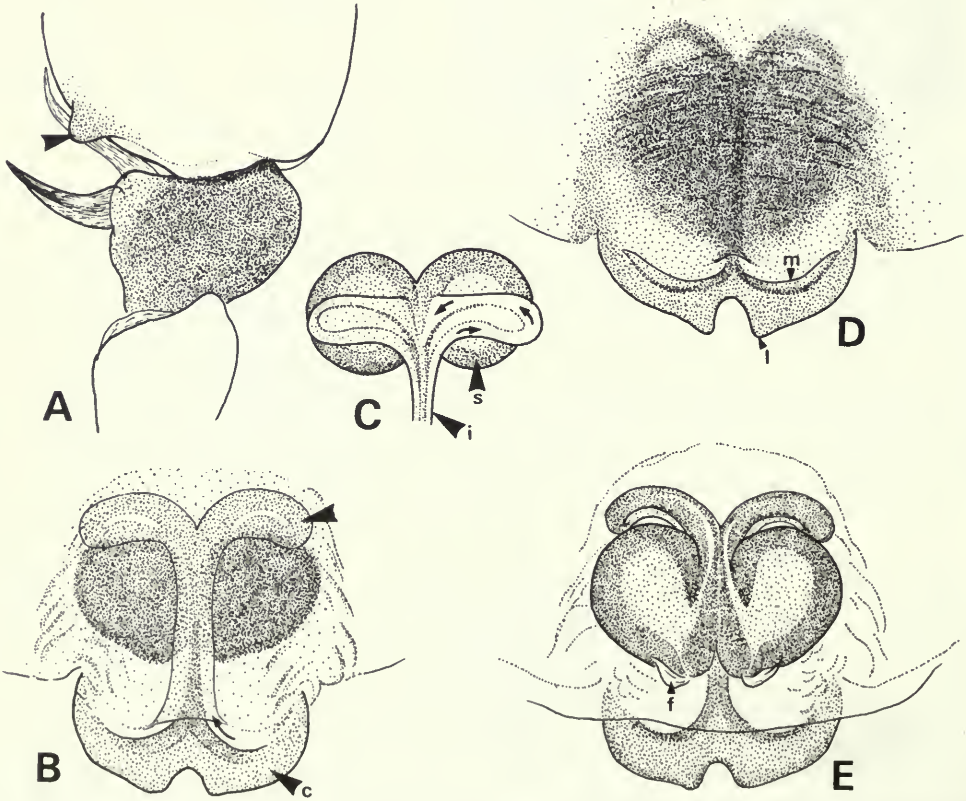

Fig. 6 *Cyrba algerina* (Lucas). ♂: A, palpal tibia, dorsal. ♀: B, vulva, outer view; C, spermathecae and introductory ducts, anterior view; D, epigyne; E, vulva, inner view. Abbreviations: c, caudal ledge; f, fertilisation duct; i, introductory duct; l, lobe of caudal ledge; m, margin of embolic guide; s, spermathecae.

are lightly suffused black and tibiae III–IV which are vaguely annulated; clothed in blackish hairs, especially legs I–II, with scattered white ones. Spination of legs I: metatarsi v 2-0-0; tibia v 2-2-2, femora d 0-2-3. *Palp*: femur and patella yellow-brown suffused black, tibia and tarsus darker; clothed in black hairs with scattered white ones. *Epigyne* (Fig. 6B–E): thinly clothed in black hairs; the distal folds of the introductory ducts characteristic of *C. bimaculata, C. legendrei* and *C. ocellata* are lacking in this species and thus never show through the integument as dark patches.

Dimensions (mm): total length 5·12; carapace length 2·36, breadth 1·7; height 1·16; abdomen length 2·64; eyes, anterior row 1·68, middle row 1·44, posterior row 1·54; quadrangle length 1·09 (46% of carapace length). *Ratios*: AM : AL : PM : PL :: 13 : 8 : 2 : 7·5; AL–PM–PL :: 9·5–6; AM : CL :: 13 : 2·5.

VARIATION. ♂ total length varies from 4·0 to 4·32 mm, carapace length 1·88–2·0 mm (ten specimens); ♀ total length 4·24–6·0 mm, carapace length 2·08–2·3 mm (ten specimens).

Males are sometimes less distinctively marked than the specimen described above. Also, females may be paler—the abdomen being creamy yellow with a somewhat speckled pattern comprised of brown-black lanceolate hairs (see Wanless, 1984).

DISTRIBUTION. Algeria; Bulgaria; Canary Islands; Corfu; Egypt; France; Greece; Guinea Bissau; Hungary; Indian Himalayas; Israel; Italy; Libya; Madeira; Mallorca; Morocco; Oman; Portugal; Sicily; Spain; Syria; Tunisia; USSR: Tadjikistan; Yugoslavia.

MATERIAL EXAMINED. **Algeria:** Heljani near Oran, Neotype ♀, ix–x. 1953, (BMNH. 1983.6.24.1); Biskra, 1♂, 2 juveniles, Keyserling coll. (BMNH. 1891.8.1.478–9). **France:** Pre Alps near Die, 2♂♂, 1♀, 25.v.1975, *P.D. Hillyard,* (BMNH); Pyrénées Orientales, Cerbére, juvenile, 23–24.vi.1962, *D. J. Clark,* (BMNH). **Libya:** Porto Bardia, 2 juveniles, iii.1927, (MZS, Firenze). **Italy:** Elba, Marciana Marina, 1♀, 17.ix–3.x.1969, *D. J. Clark*; Sicily, Messina, 3♂♂, 22.iii.1965, *M. Clifton,* (BMNH). **Greece:** Crete, 1♀, Akrotivi, 1♂, Phaestos, iv.1979, *J. & F. Murphy;* Terracina, 1♂, *T. R. R. Stebbing,* (BMNH. 1927.8.13.1180). **Portugal:** Algarve, under stones, 1♂, 1♀, *J. & F. Murphy* BMNH). **Spain:** Canary Islands, Tenerife–Grand Canary–Fuerteventura, mixed ♂♂, ♀♀, juveniles, (MNHN, Paris. 14127); Arucas, 800–1000 ft, 1♀, 25.vii.1925, (MCZ, Harvard); Torremolinos, 1♂, iv.1975, *P. D. Hillyard;* Mallorca, Deyá, 1♂, vi.1971, *B. Graves*; Mallorca, Puerto Soller, juveniles, 9–12.x.1966, *D. J. Clark*; Puerto Pollensa, juveniles, x.1968, *D. J. Clark,* (BMNH). **Yugoslavia:** Dalmatia, 1♂, 2 juveniles, Keyserling coll. (BMNH. 1891.8.1.476–477).

Cyrba ocellata (Kroneberg) sp. rev.

(Figs 7A–F; 8A–G; 18A–C)

Euophrys ocellata Kroneberg, 1875: 48, ♀. LECTOTYPE ♀ (here designated) USSR, Samarkand, (NR. Stockholm) [examined]. Kroneberg, 1888: 191. [Thorell, 1890: 83, incorrectly synonymised with *C. algerina* (Lucas)].

Cyrba micans Simon, 1885: 22, ♂. LECTOTYPE ♂ (here designated) India, (MNHN, Paris) [examined]. Simon, 1901: 447, 448; 1903: 731. Roewer, 1954: 985. Bonnet, 1956: 1339. Prószyński, 1971: 396; 1978: 16. **Syn. n.**

Stasippus inornatus Thorell, 1887: 375, ♀. LECTOTYPE ♀ (here designated) Burma (NR. Stockholm). [Thorell, 1890: 83, incorrectly synonymised with *C. algerina* (Lucas)]. **Syn. n.**

Vindima maculata Thorell, 1895: 348, ♂. Holotype ♂, Burma (BMNH 1895.9.21.1057) [examined]. Roewer, 1954: 1703, Bonnet, 1959: 4797.

Cyrba flavimana Simon, 1899: 103, ♀. LECTOTYPE ♀ (here designated) (MNHN. Paris) [examined]. Simon, 1901: 448. Roewer, 1954: 985. Bonnet, 1956: 1339. Prószyński, 1971: 396; 1978: 16[=*C. micans*].

Astia maculata: Simon, 1901: 436. Roewer, 1954: 968. Bonnet, 1955: 768. Prószyński, 1971: 379. **Syn. n.**

Cyrba tadzika Andreeva, 1969: 89, ♂, ♀, [not examined]. Prószyński, 1971: 396, [=*C. micans*].

C. tadzhika: Prószyński, 1971: 396 [lapsus calami].

DIAGNOSIS. Males of *C. ocellata* are most likely to be confused with those of *C. legendrei,*

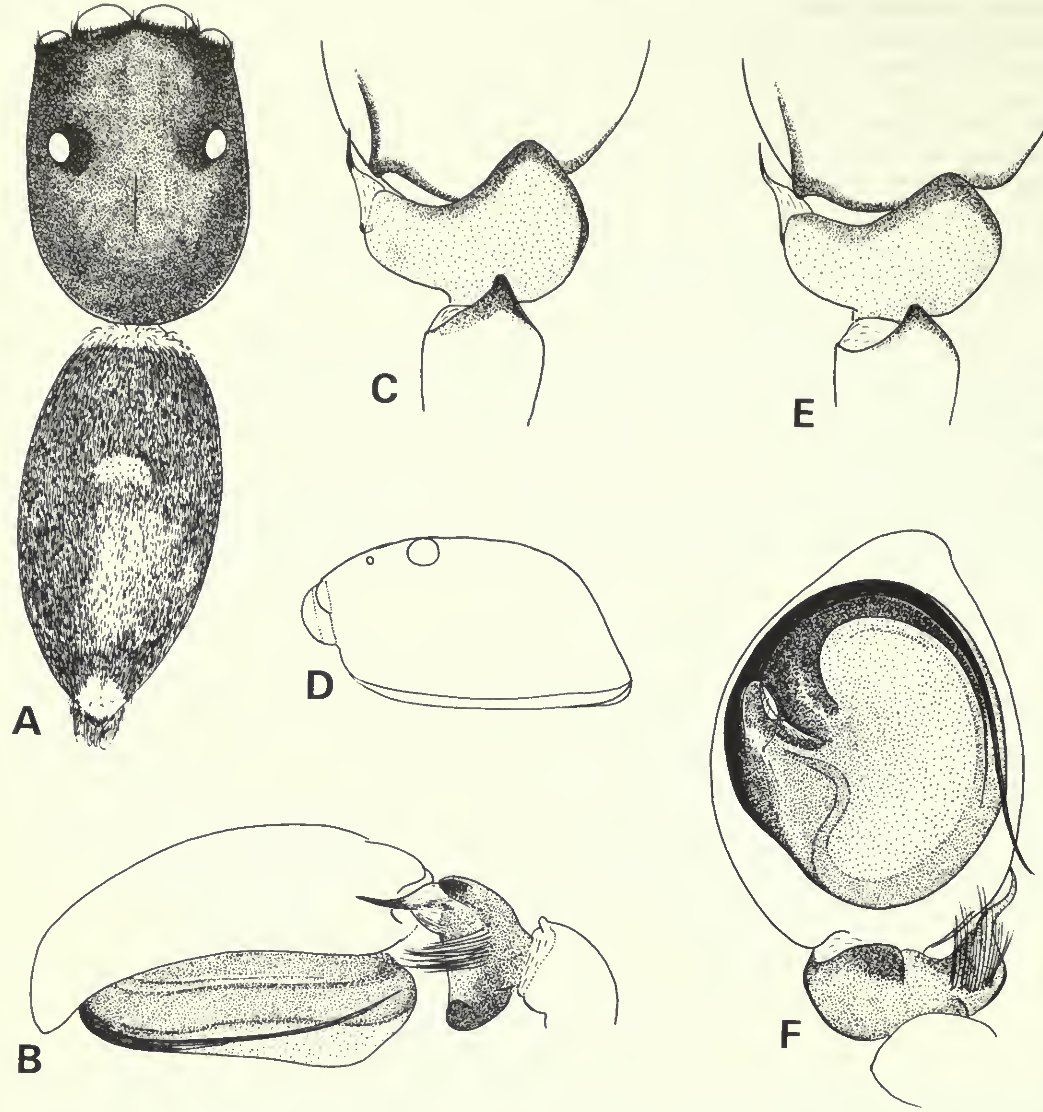

Fig. 7 *Cyrba ocellata* (Kroneberg). ♂ from Sri Lanka: A, dorsal; C, palpal tibia, dorsal; D, carapace, lateral. Lectotype ♂ [*C. micans*]: B, palp, retrolateral; E, palpal tibia, dorsal; F, palp, ventral.

but can be distinguished by the absence of a longitudinal abdominal stripe and ledge supporting the posterior spur of the retrolateral tibial apophysis (Fig. 8A, B). Females on the other hand could be confused with those of *C. algeria, C. bimaculata* or *C. legendrei* since the epigynes are rather similar to one another. *C. ocellata* is however, readily separated from *algerina* by the presence of large distal lobes on the curving part of the introductory ducts (Fig. 8E, F) and from both *bimaculata* and *legendrei* by the form of the embolic guides which extend laterally (Fig. 8C–E, arrowed) rather than anteriorly.

MALE from Sri Lanka, in good condition. *Carapace* (Fig. 7A, D): brown suffused and mottled black with an iridescent sheen under some angles of illumination; generally clothed in grey-black shining hairs with a thin white haired marginal band and whitish hairs on sides below anterior lateral and posterior median eyes, and base of thoracic slope. *Eyes*: with black surrounds; fringed by grey-black and white hairs. *Clypeus*: clothed in whitish hairs with fringe of stiff blackish hairs interrupted medially by group of long whitish ones. *Chelicerae*: brown with black markings; thinly covered in white hairs basally with fine blackish ones along inner margins; promargin with three teeth, retromargin with five. *Maxillae*: yellow-brown tinged black with paler inner margins. *Labium*: yellow-brown with paler edging. *Sternum and coxae*: yellow-brown suffused black; shiny with whitish hairs. *Abdomen*: yellow-brown suffused and mottled black; clothed in black lanceolate hairs with conspicuous white haired patches basally, medially, on lateral sides and around spinnerets; mytiliform field inconspicuous; spinnerets blackish. *Legs:* femora blackish/iridescent, clothed in black hairs with longitudinal white haired stripes; other segments yellow-brown suffused with some black, clothed in black and clear whitish hairs forming vague longitudinal stripes on posterior tibiae; spines moderately strong and numerous. Spination of legs I: metatarsi v 2-0-1, p 1-0-2; r 1-0-2; tibiae v 2-1-3, p 1-0-2, d 0-1-0, r 1-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Palp* (Fig. 8B): femur and patella yellow-brown suffused black with covering of whitish hairs, tibia and cymbium much darker with black and some white hairs.

Dimensions (mm): total length 4·72; carapace length 2·08, breadth 1·48, height 1·12; abdomen length 2·6; eyes, anterior row 1·32, middle row 1·12, posterior row 1·26; quadrangle length 0·88 (42% of carapace length). *Ratios*: AM : AL : PM : PL :: 10·5 : 6 : 1·5 : 6; AL–PM–PL :: 7–5; AM : CL :: 10·5 : 4.

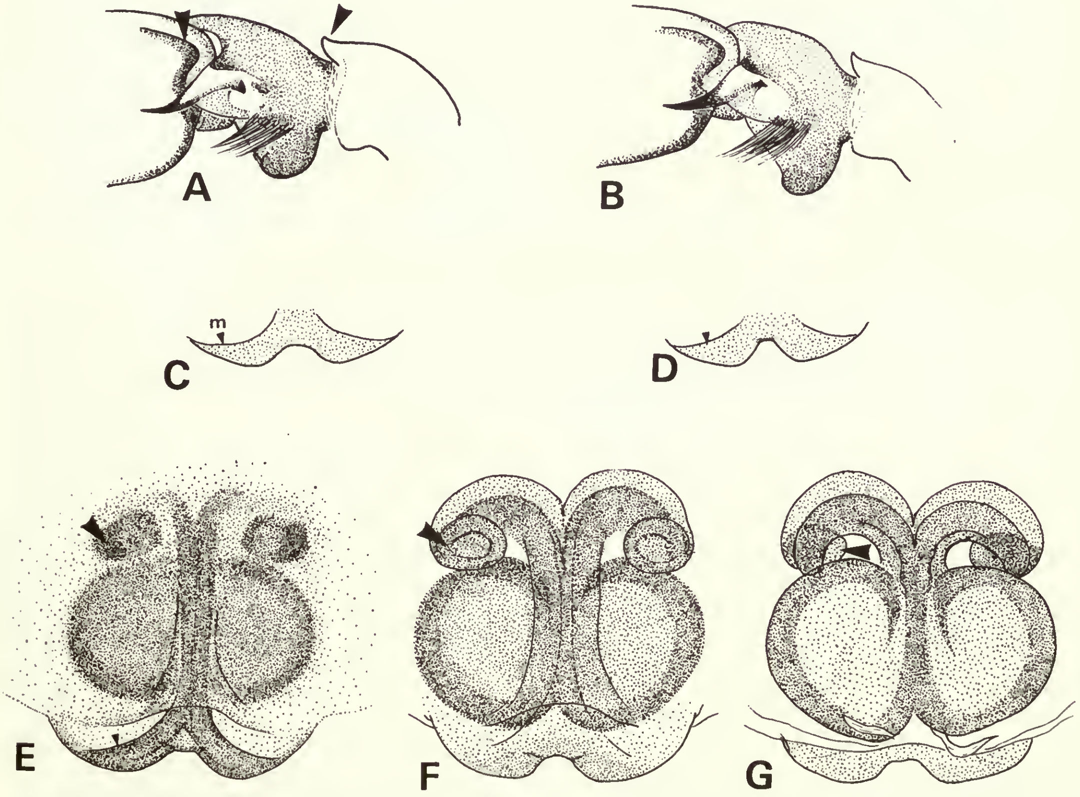

Fig. 8 *Cyrba ocellata* (Kroneberg). A, ♂ from Kenya, palpal retrolateral tibial apophysis. B, ♂ from Sri Lanka, palpal retrolateral tibial apophysis showing variation in basal spur development. C, D, ♀: caudal ledge variation. E, ♀ lectotype [*C. flavimanis*], epigyne. ♀: F, vulva outer view; G, vulva, inner view.

Female from Sri Lanka, in good condition. Similar to ♂, but lacking conspicuous white markings. *Carapace*: orange-brown mottled with some black with blackish eye region and an iridescent sheen under some angles of illumination; clothed in grey-black shining hairs and scattered bristles (evidently rubbed in ♂). *Eyes*: posteriors fringed by greyish hairs with dull amber ones around anteriors, also above anteriors numerous scattered bristles. *Clypeus*: fringed by greyish and dull amber hairs. *Chelicerae*: amber suffused with some black, shiny with scattered grey-black hairs; promargin with three teeth, retromargin with six. *Maxillae, labium, sternum and coxae*: more or less as in ♂ except for grey-black hairs on coxae and sternum. *Abdomen*: yellow-brown suffused and mottled black; clothed in greyish lanceolate hairs and black bristles with obscure creamy spots posteriorly and on either side of anal tubercle. *Legs*: yellow-brown suffused with some black especially on femora; spines moderately strong, most numerous on posterior legs. Spination of legs I: metatarsi v 2-0-0; tibiae v 2-2-2; femora d 0-2-3, p 0-0-1. *Epigyne*: as in Fig. 8E, but darker.

Dimensions (mm): total length 4·16; carapace length 1·76, breadth 1·36, height 0·98; abdomen length 2·4; eyes, anterior row 1·34, middle row 1·17, posterior row 1·28; quadrangle length 0·95 (53% of carapace length). *Ratios*: AM : AL : PM : PL ::10·5 : 6·5 : 1·5 : 6; AL–PM–PL :: 7–5; AM : CL :: 10·5 : 1.

Variation. ♂ total length varies from 4·36 to 5·12 mm, carapace length 1·88–2·36 mm (ten specimens); ♀ total length 4·08–6·1 mm, carapace length 1·76–2·44 mm (ten specimens).

Freshly preserved specimens are usually dark whereas older material is inevitably bleached, often yellow-brown or orange-brown with only faint blackish mottling on the abdomen. The male palpal retrolateral tibial apophysis also seems to vary. In the lectotype ♂ of *C. micans* (Fig. 7B) there is in lateral view only a slight suggestion of a bleached backward pointing spur which is however, more evident when viewed slightly from above. Additional material from Kenya and Sri Lanka possess even larger spurs (Fig. 8A, B) which seem quite distinct when compared with the lectotype of *micans*. They were initially believed to represent another taxon, but a series of males from Vietnam shows that the development of the spur is variable.

Distribution, Australia; Bhutan; Burma; French Somaliland; India; Indonesia; Kalimantan; Java; Kenya; Nepal; Philippines; Singapore; Sri Lanka; Sumatra; Thailand; USSR; Tadjikistan; Vietnam.

Material examined. **Australia:** Wilson Island, Great Barrier Reef, 1♀, 9.ix.1969, *H. Heatwole*, (Queensland Museum). **Burma:** Tharrawaddy, holotype ♂, [of *Vindima maculata*] *E. W. Oates*, (BMNH. 1895.9.21.1057); Bhamo, syntype [of *Stasippus inornatus*] *L. Fea*, leg, presented by G. Doria, (NR, Stockholm 6521). **French Somaliland:** Djibouti, 1♂, vii.1974. *P. Leriche*, (MRAC, Tervuren. 146.264). **India:** Collegal, Coimbatoore District, lectotype ♂, [of *C. micans*] M. A. Theobald, (MNHN, Paris, 7671). **Indonesia:** Kalimantan, International Timber Corporation of Indonesia, 12 km North of Balikpapan, 1♀, 19.x.1975, *R. Thomson* (BMNH). **Java:** 1 ♂, *Kulczyński* collection, (MNHN, Paris. 15780). **Kenya:** Elyic Point, Lake Rudolf, 1♂, iii.1920, *J. Miskell*, (BMNH). **Philippines:** Antipolo, 1♂, *E. Simon*, (MNHN, Paris. 15780). **Sri Lanka:** Wirawila, Hambantoto District, Mike Northways Sanctuary, 1♂, on tree trunk. 19.x.1982, *F. R. Wanless;* Nilaveli, Trincomalee District, 1♀, dry scrub jungle, on vegetation, 27.x.1982, *F. R. Wanless*, (DNM, Colombo); Pollebedde, Maha-Oya District, 1♂, 16.viii.1963, *M. Speight*, Univ. Lond. Ceylon Expd. (BMNH). **Singapore:** 1♀, (MNHN, Paris. 12674). **Sumatra:** lectotype ♀ [of *C. flavimanus*] J.-L. Weyers, (MNHN, Paris, 16271). **Thailand:** Chieng Mai Province, Fang Horticultural Exp. Stn. 550–600 m. 1♀, 20.x.1981 (UZM, København). **USSR:** Samarkand, lectotype ♀, [of *Euophrys ocellata*] *Fedtschenko & Kroneberg*, (NR, Stockholm, Thorell collection, 251/1612c).

Cyrba legendrei sp. n.

(Fig. 9A–J)

Diagnosis. Males of *C. legendrei* are similar to those of *C. ocellata*, but may be distinguished by the presence of a longitudinal abdominal stripe (i.e. in unrubbed specimens) and ledge which appears to support the posterior prong of the retrolateral tibial apophysis (Fig. 9D, arrowed). Females resemble those of *C. algerina, C. bimaculata* and *C. ocellata.* They are separated from *algerina* by the absence of marked wrinkling in the epigynal area and presence of distal folds on the curving part of the introductory ducts (Fig. 9H, I); from *bimaculata* by the poorly developed lobes of the caudal ledge (Fig. 9H) and from *ocellata* by the anteriorly curved margins of the embolic guides (Fig. 9H, arrowed).

C. legendrei also seems to have a rather limited geographical distribution and is only known to occur in Madagascar and the Comoro Islands.

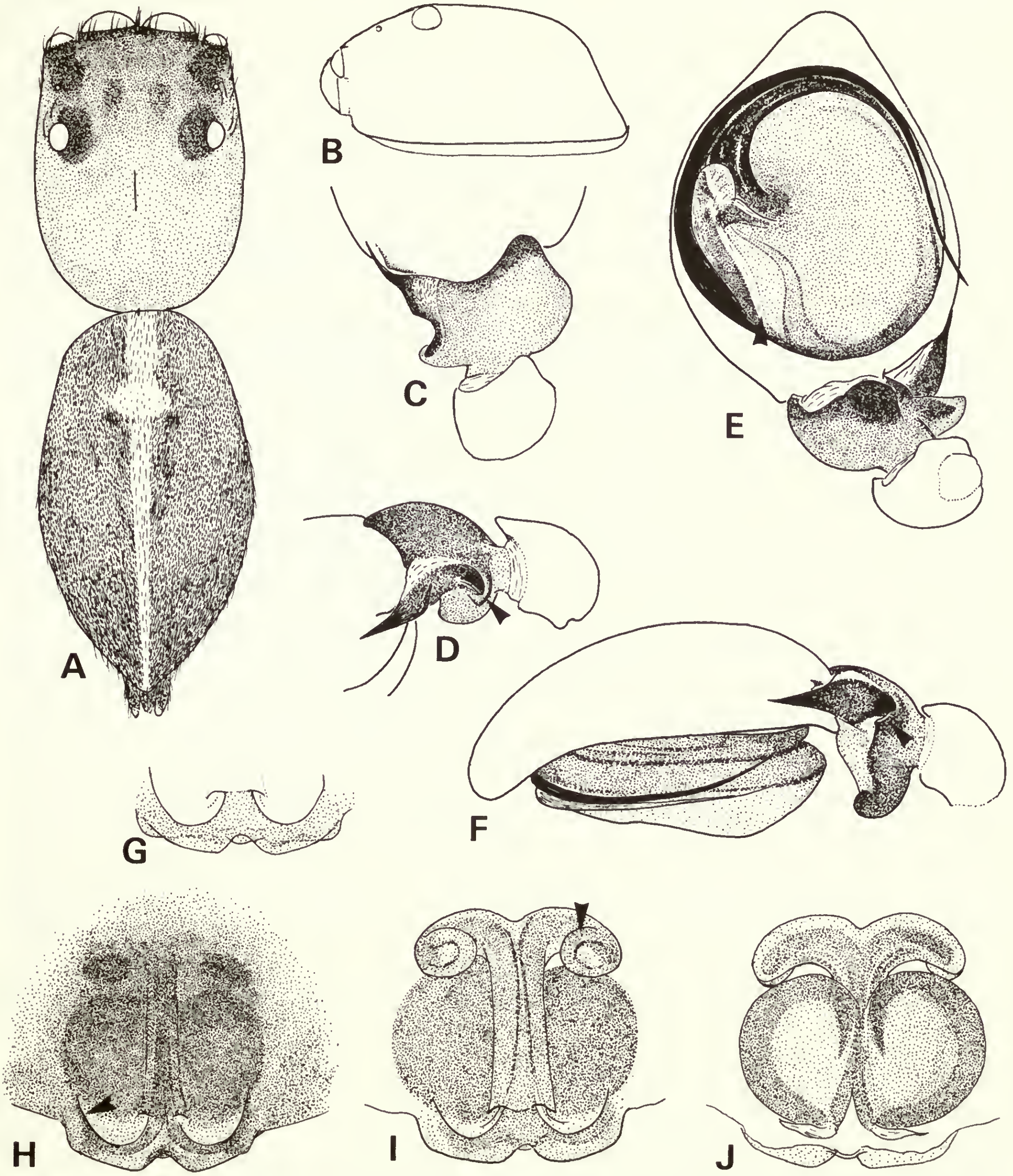

Fig. 9 *Cyrba legendrei* sp. n., holotype ♂: A, dorsal; B, carapace, lateral; C, palpal tibia, dorsal; D, palpal tibia, dorsolateral; E, palp, ventral; F, palp, retrolateral. Paratype ♀: G, caudal ledge cleared, viewed slightly from behind; H, epigyne; I, vulva, outer view; J, vulva, inner view.

MALE HOLOTYPE, in good condition. *Carapace* (Fig. 9A, B): pale orange-brown lightly suffused black in eye region; clothed in recumbent fine whitish and pale golden hairs with scattered bristles dorsally. *Eyes*: with black surrounds; fringed by whitish hairs. *Clypeus*: amber lightly mottled black; thinly covered in whitish and black hairs. *Chelicerae*: weakly iridescent; yellow-brown with blackish markings, clothed in fine scattered hairs; promargin with three teeth, retromargin with five. *Maxillae*: grey to yellow-brown with whitish inner distal margins. *Labium*: grey with yellowish grey margins. *Sternum*: yellow-brown faintly tinged black with darker margins; shiny, clothed in stiff brownish hairs. *Coxae*: colour as sternum. *Abdomen*: generally yellow-brown; covered in recumbent brown-black lanceolate hairs and fine scattered bristles with dorsal longitudinal stripe clothed in whitish hairs, ventrally a pair of yellow-brown stripes converging posteriorly; mytiliform field obscure; spinnerets grey-black with whitish tips. *Legs*: legs I femora yellow-brown with black prolateral/ventral patches, other segments orange-brown suffused with some black on dorsum of tibiae, metatarsi and tarsi, thinly clothed in black, grey and some white hairs; legs II similar to I except black markings less extensive; legs III and IV generally orange-brown with vague longitudinal stripes comprised of black and whitish hairs especially on femora, patella and tibiae of legs IV; spines moderately strong and numerous. Spination of legs I: metatarsi v 2-0-0, p 0-1-1, d 0-0-1, r 0-1-1; tibiae v 2-2-2, p 1-0-1, r 0-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-2, p 0-0-1. *Palp* (Fig. 9C–F): basal retrolateral flange of cymbium small compared with that of *C. ocellata.*

Dimensions (mm): total length 4·24; carapace length 1·86, breadth 1·36, height 1·0; abdomen length 2·36; eyes, anterior row 1·24, middle row 1·08, posterior row 1·18; quadrangle length 0·8 (43% of carapace length). *Ratios*: AM : AL : PM : PL :: 9·5 : 5·5 : 1·0 : 5·5; AL–PM–PL :: 6·5 : 5; AM : CL :: 9·5 : 4·0.

FEMALE PARATYPE, in good condition, *Carapace*: orange-brown lightly suffused with some black; clothed in recumbent greyish hairs and scattered bristles with vague longitudinal stripes of shining hairs on thoracic slope. *Eyes*: laterals with black surrounds; fringed by greyish and buff hairs. *Clypeus*: clothed in buff hairs. *Chelicerae*: orange-brown with sooty markings; weakly iridescent, clothed in scattered fine grey-black hairs; promargin with three teeth, retromargin with six. *Maxillae and labium*: orange-brown lightly tinged black with whitish yellow tips. *Sternum and coxae*: orange-brown tinged black with scattered brown hairs. *Abdomen*: yellowish brown lightly tinged with some black; clothed in recumbent light brownish grey hairs and scattered black bristles; ventrally a pair of converging lateral stripes as in ♂; mytiliform field obscure; spinnerets blackish with paler tips. *Legs*: generally orange-brown suffused and mottled black; spines moderately strong, most numerous on posterior legs. Spination of legs I: metatarsi v 2-0-0; tibiae v 2-2-2, femora d 0-2-2, p 0-0-1. *Palp*: femora and patella orange-brown tinged with some black, other segments darker. *Epigyne* (Fig. 9H–J): the caudal ledge bears a slight recess on either side—best seen when the cleared epigyne is viewed from above and slightly behind (Fig. 9G).

Dimensions (mm): total length 4·96; carapace length 2·0, breadth 1·48, height 1·04; abdomen length 3·12; eyes, anterior row 1·36, middle row 1·24, posterior row 1·36; quadrangle length 0·88 (44% of carapace length). *Ratios*: AM : AL : PM : PL :: 10·5 : 6 : 1·3 : 6; AL–PM–PL :: 7–5; AM : CL :: 10·5 : 2.

VARIATION. Females vary from 4·2 to 5·28 mm total length, 1·84–2·4 mm carapace length (five specimens).

DISTRIBUTION. Comoro Islands; Madagascar.

MATERIAL EXAMINED. **Grande Comore:** Grotte Dubois, paratype ♀, xi.1954, *J. Millot,* (MNHN, Paris). **Madagascar:** Manjakatompo, Mt. Ankaratra, holotype ♂, paratype ♀, ii.1967, *R. Legendre,* (MNHN, Paris); Prov. Tananarive, Tziazompaniry, a small water fall S. of Tananarive, paratype ♀, iii.1958, *R. Legendre,* (BMNH, 1983.4.6.1); F. Ambodivoangy, forest near Maroantsetra, E. Madagascar, paratype ♀, 1948, *J. Millot,* (MNHN, Paris); Environs of Tananarive, paratype ♀, under stones, 6.xi.1927, *R. Decary*—Entrée 6, 1928, (MNHN, Paris); paratype ♀, viii.1947, locality illegible (MNHN, Paris).

ETYMOLOGY. This species is named after Professor R. Legendre, Université des Sciences et Techniques du Languedoc, Montpellier.

Cyrba bimaculata Simon

(Figs 1; 10A–L: 17E, F; 22E)

Cyrba bimaculata Simon, 1886: 392, ♀. LECTOTYPE ♀ (here designated) Angola, (MNHN, Paris) [examined]. Simon, 1901: 448. Roewer, 1954: 985. Bonnet, 1956: 1339. Prószyński, 1971: 396.

DIAGNOSIS. Males of *C. bimaculata* are easily recognised by the combined presence of an embolic prong and simple retrolateral tibial apophysis (Fig. 10F, I). Females are more difficult, but may be separated from *C. algerina* by the absence of marked wrinkling in the epigynal area and presence of small lobes on the curving parts of the introductory ducts (Fig. 10J, K); from *C. ocellata* by the anteriorly curved margins of the embolic guides (Fig. 10J, K) and from *C. legendrei* by the relatively pronounced lobes of the caudal ledge (Fig. 10J).

MALE from Kenya, formerly undescribed, in good condition. *Carapace* (Fig. 10C, D): yellow-brown with sooty markings in quadrangle; clothed in recumbent bright orange hairs. *Eyes*: laterals with black surrounds; fringed by whitish and bright orange hairs with scattered black bristles above anteriors. *Clypeus*: yellow-brown clothed in whitish hairs with black patches clothed in grey-black hairs below each anterior median and anterior lateral eye. *Chelicerae*: pale yellow-brown lightly speckled with some black; shiny, thinly clothed in fine whitish hairs with blackish ones along inner distal margins; promargin with three teeth, retromargin with five. *Maxillae*: pale yellow-brown. *Labium*: yellow-brown. *Sternum and coxae*: light yellow-brown, clothed in fine pale orange and greyish hairs. *Abdomen*: pale yellow-brown covered in recumbent bright orange hairs and scattered black bristles; mytiliform field relatively distinct; spinnerets greyish with black hairs. *Legs* (Fig. 10B): pale yellow-brown clothed in bright orange hairs with tibiae, metatarsi and base of tarsi suffused and streaked black with covering of orange and grey hairs the latter forming an indistinct fine ventral fringe on metatarsi III and IV; spines moderately strong and numerous. Spination of legs I: metatarsi v 0-2-0, p 0-1-2, r 0-1-2; tibiae v 2-2-2, p 1-0-1, r 1-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-3. *Palp* (Fig. 10E, F, I): femora yellow-brown clothed in orange hairs except for blackish prolateral markings distally; patellae greyish yellow with orange hairs basally becoming dark with black hairs distally; other segments brown suffused black with black hairs except for greyish scopula on cymbial tip.

Dimensions (mm): total length c. 4·3 (bent); carapace length 1·98, breadth 1·52, height 1·12; abdomen length 2·34; eyes, anterior row 1·4, middle row 1·24, posterior row 1·38; quadrangle length 0·99 (50% of carapace length). *Ratios*: AM : AL : PM : PL :: 11 : 6·8 : 1·5 : 6·3; AL–PM–PL :: 9–5·6; AM : CL :: 11 : 5·3.

FEMALE from Kenya, rubbed, but otherwise in good condition. *Carapace*: light orange-brown, weakly iridescent under some angles of illumination irregulary and scantily clothed in greyish lanceolate hairs. *Eyes*: laterals with black surrounds, fringed by pale amber hairs. *Clypeus*: clothed in pale amber hairs. *Chelicerae* (Fig. 10H): yellow-brown lightly suffused with some black; shiny with scattered light greyish hairs. *Maxillae and labium*: generally as in ♂. *Sternum* (Fig. 10G): yellow-brown with vague darker margins; shiny; thinly clothed in grey hairs. *Coxae*: yellow-brown with scattered grey hairs. *Abdomen*: whitish yellow tinged grey; rubbed; mytiliform field indistinct; spinnerets whitish yellow suffused black. *Legs*: moderately long and slender with metatarsi and tibiae of legs I–II a little swollen (Fig. 10A); generally light orange-brown, but metatarsi I and tibiae I suffused black; spines moderately strong, most numerous on posterior legs. Spination of legs I: metatarsi v 2-0-0; tibiae v 2-2-2; femora d 0-2-2, p 0-0-1. *Epigyne* (Fig. 10J–L).

Dimensions (mm): total length c. 5·12 (pedicel stretched); carapace length 1·84, breadth 1·44, height 1·04; abdomen length 3·08; eyes, anterior row 1·44, middle row 1·28, posterior

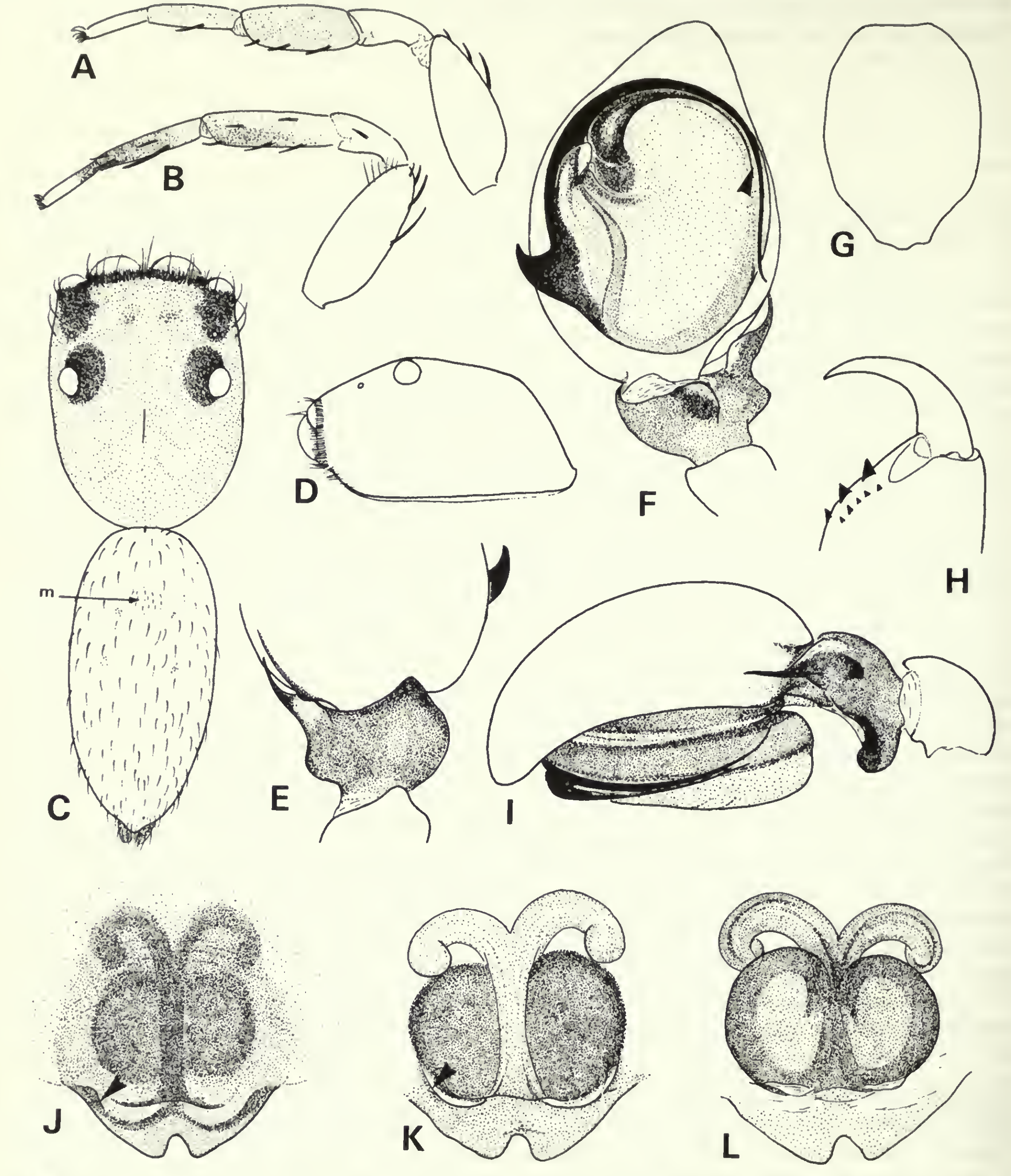

Fig. 10 *Cyrba bimaculata* Simon, ♂: B, leg I; C, dorsal; D, carapace, lateral; E, palpal tibia, dorsal; F, palp, ventral; I, palp, retrolateral. ♀: A, leg I; G, sternum; H, chelicera; J, epigyne; K, vulva, outer view; L, vulva, inner view. Abbreviation: m, mytiliform field.

row 1·4; quadrangle length 0·92 (50% of carapace length). *Ratios*: AM : AL : PM : PL :: 12 : 6·4 : 1·2 : 6; AL–PM–PL :: 8–6; AM : CL :: 12 : *ca.* 2.

VARIATION. Males vary from 4·04 to 4·44 mm total length, 1·76–1·98 mm carapace length (three specimens); females vary from 4·7–5·5 mm total length, 1·84–2·04 mm carapace length (six specimens).

The integument varies from whitish in the lectotype to dark brown in a specimen from the Cameroons. Also, the bright orange hairs, which are easily rubbed, fade to light brown or amber after three or four years preservation.

DISTRIBUTION. Angola; Burundi; Cameroon; Kenya; Nigeria; Zaire.

MATERIAL EXAMINED. **Angola:** Cabinda, route Dinge-Buco, under bark of living trees, 1♀, 30.v.1973, *A. de Barros Machado,* Ang. 23375.9; Landana, lectotype ♀, *L. Petit,* (MNHN, Paris, 7644). **Burundi:** Plaine de la Ruzizi, Secteur de Gihanga, 900 m, dans terreau de bambous, v.1966, *S. Ndani,* MT 130590 & 130600, (MRAC, Tervuren). **Cameroon:** 1949–50, 1♀. **Kenya:** Kilifi, leaf litter, 1♂, 1♀, iix.1980, *J. & F. Murphy,* 9137. **Nigeria:** Gambari, Forest Reserve, Ibadan, 2♂♂, 3♀♀, 8.iv.1973, *A. Russell-Smith,* (BMNH). **Zaire:** Terr. Uvira: Lake Tanganyika, 'banks', 2♂♂, vi.1958, *N. Leleup,* MT. 112626; Kivu, Itombwe, (Kakazi) moyenne Masunga, vestiges ole forêt Heliophile, 1200 m, 1♀, vi.1961, *N. Leleup,* B152; Kivu, ruiss entre Kalimabenge-Kambekulu, sous des pierres, 1♂, v.1962, *R. Kiss,* MT. 122799; Ile de M'Boko, Kivu, 1♀, 6.ii.1957, *N. Leleup,* MT. 91347 & 91351. Province Moyen Congo, Bumba, 1♂, I.1940, *Saeger,* MT. 20081. Province Kasi, Kassi, Mwadia, 1♂, *Fourche,* MT. 11983; Prov. Kivu, Komi, 5♂♂, 2♀♀, *J. Ghesquiere,* MT. 11859. (MRAC, Tervuren).

Cyrba boveyi Lessert

(Fig. 11A–F)

Cyrba boveyi Lessert, 1933: 145, ♂. Holotype ♂, Angola; paratype ♂, Mozambique, (MHN, Geneva), [examined]. Lessert, 1936: 288. Roewer, 1954: 985. Bonnet, 1956: 1339. Prószyński, 1971: 396. Cutler, 1976: 131.

DIAGNOSIS. A distinctive species easily recognised by the fan-like retrolateral tibial apophysis in males (Fig. 11B, C) and presence of a transverse epigynal suture in females (Fig. 11D, arrowed).

MALE HOLOTYPE, bleached otherwise in good condition. General habitus typical of genus. *Carapace*: pale yellowish orange with sooty markings in quadrangle and fine whitish hairs on sides; dorsum rubbed. *Eyes*: laterals with black surrounds; fringed by whitish hairs with scattered bristles above anterior medians and anterior laterals. *Clypeus*: covered in whitish hairs. *Chelicerae*: pale whitish yellow faintly tinged with some black; clothed in fine hairs along inner margins; pro- and retromargins with three teeth. *Maxillae, labium, sternum and coxae*: whitish yellow, shiny. *Abdomen*: whitish yellow faintly suffused and mottled with some black. *Legs*: generally whitish yellow except for tibiae I which are faintly tinged black and clothed in light amber hairs. Spination of legs I: metatarsi v 2-0-2, p 0-1-0, d 0-0-1; tibiae v 2-2-2, p 0-0-1, d 1-1-0, r 0-0-1; patellae p 0-1-0, r 0-1-0; femora d 0-2-3. *Palp* (Fig. 11A–C): the patellar apophysis is probably more conspicuous in fresh material.

Dimensions (mm): total length 4·4; carapace length 1·92, breadth 1·44, height 0·99; abdomen length 2·4; eyes, anterior row 1·42, middle row 1·2, posterior row 1·32; quadrangle length 0·92 (47% of carapace length). *Ratios* : AM : AL : PM : PL :: 11 : 6·3 : 1·5 : 6·3; AL–PM–PL :: 7–5; AM : CL :: 11 : 3.

FEMALE from Kenya, formerly undescribed, in good condition. General habitus typical of genus. *Carapace*: orange-brown lightly suffused and mottled with some black; iridescent under some angles of illumination; clothed in recumbent shining light greyish hairs and scattered bristles. *Eyes*: with black surrounds; fringed by light amber and whitish hairs. *Clypeus*: thinly clothed in dull whitish hairs and scattered bristles. *Chelicerae*: orange-brown lightly tinged with some black; shiny with scattered grey hairs; promargin with three teeth, retromargin with four. *Maxillae*: orange-brown faintly tinged black with whitish inner margins. *Labium*: orange-brown lightly tinged black with whitish tip. *Sternum*: pale orange-brown faintly suffused black; shiny with scattered pale greyish hairs. *Coxae*: colour as sternum except posteriors lighter. *Abdomen*: greyish yellow clothed in recumbent grey and light yellow-brown hairs with scattered bristles; mytiliform field obscure. *Legs*: generally orange-brown lightly suffused with some black; thinly clothed in greyish black hairs; spines

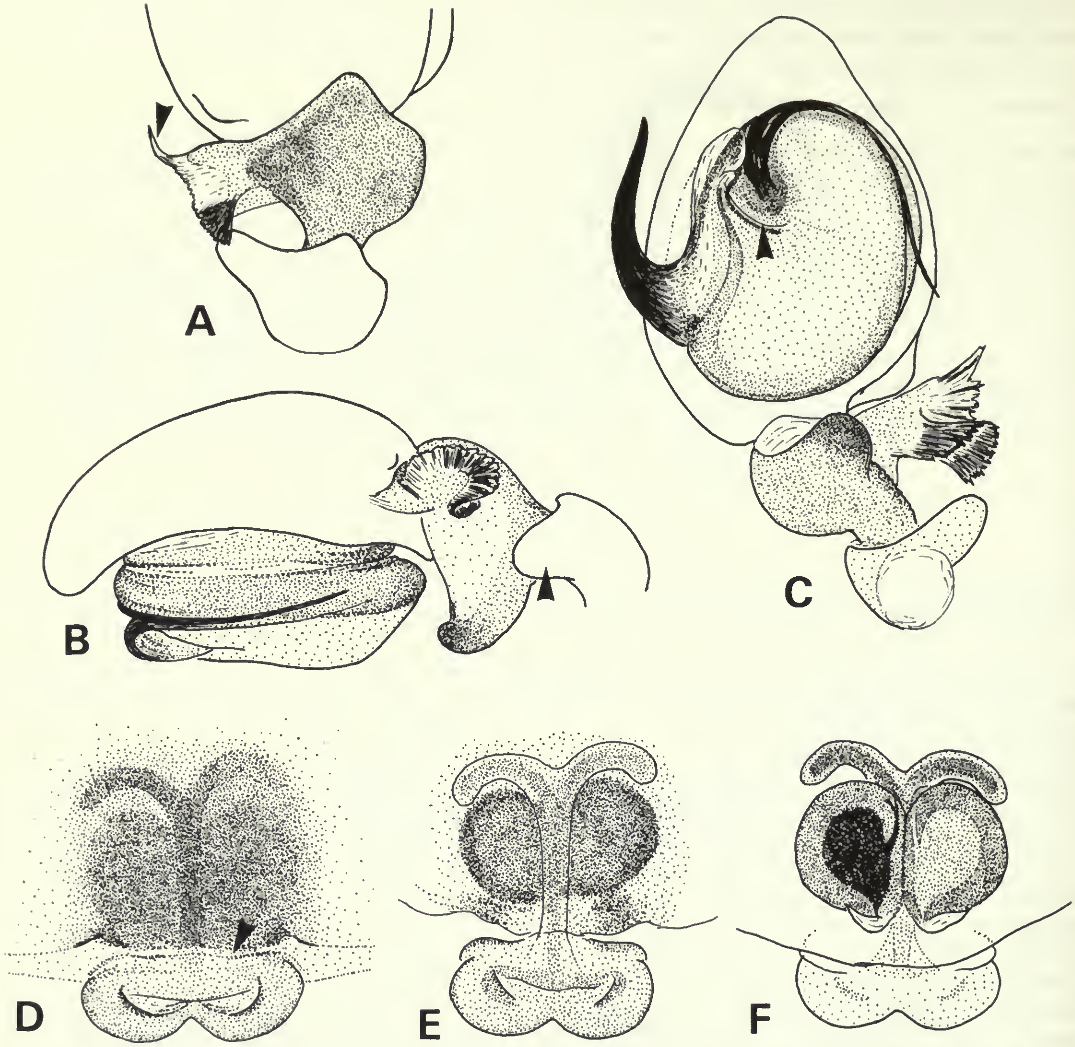

Fig. 11 *Cyrba boveyi* Lessert, paratype ♂: A, palpal tibia, dorsal. Holotype ♂: B, palp, retrolateral; C, palp, ventral. ♀: D, epigyne; E, vulva, outer view; F, vulva, inner view.

moderately strong, most numerous on posterior legs. Spination of legs I: metatarsi v 2-0-0; tibiae v 2-2-2; femora d 0-0-2, p 0-0-1 *Palp*: light brownish with tarsus and tibia orange-brown faintly tinged black. *Epigyne* (Fig. 11D–F): the channels leading into and out of the spermathecae are unusually clear in this specimen.

Dimensions (mm): total length 5·16; carapace length 2·16, breadth 1·64, height 1·12; abdomen length 2·8; eyes, anterior row 1·64, middle row 1·36, posterior row 1·53; quadrangle length 1·08 (50% of carapace length). *Ratios*: AM : AL : PM : PL ::13 : 7·5 : 1·4 : 7; AL–PM–PL :: 8·5–5·5; AM : CL :: 13 : 2.

Variation: Although damaged the retrolateral tibial apophysis of the paratype male shows that the distal prong (Fig. 11A, arrowed) has broken off in the holotype.

Distribution. Angola; Kenya; Mozambique.

Material examined. **Angola:** Chimporo, holotype ♂, xi.1928, *Monard Collection,* (MHN, Geneva).

Kenya: Baringo, Central Island, grubbing in grass near hot springs, 31.vii.1974, *J. & F. Murphy,* 3821, (BMNH). **Mozambique:** Vila Pery, Paratype ♂, x.1927, *M. P. Lesne,* (MHN, Geneva).

REMARKS. Matching males with females has been difficult, for example, there were initially three unaccompanied females any of which could belong with *C. boveyi,* known only from the male. The female selected has marginally the most unusual epigyne and in this sense agrees with *boveyi* which has the most unusual palp. The geographical distribution also marginally favours the female selected, but it nevertheless remains to be seen if the match is correct.

Cyrba nigrimana Simon

(Fig. 12A–G)

Cyrba nigrimanus Simon, 1900: 389, ♀. LECTOTYPE ♀. PARALECTOTYPES 3♀♀ (here designated) S. Africa (MNHN, Paris & MCZ, Harvard) [examined]. Simon, 1901: 447, 448.
C. nigrimana: Roewer, 1954: 985. Bonnet, 1956: 1339. Prószyński, 1971: 396. Cutler, 1976: 131.

REMARKS. Four females and one juvenile labelled '20124 Cyrba nigrimanus E.S. Pretoria!' in the collections of MNHN, Paris are undoubtedly syntypes and agree with another female in the collections of MCZ, Harvard. The later specimen labelled '83 Cyrba nigrimana E. Simon, Transvaal, 4123, from E. Simon' is almost certainly part of the type series and is accordingly included amongst the paralectotype designations.

DIAGNOSIS. *C. nigrimana* known only from females is easily recognised by the darkened lateral slits of the epigynal area (Fig. 12E, arrowed).

MALE. Unknown.

FEMALE LECTOTYPE, in fair condition. *Carapace* (Fig. 12A, G): orange-brown with paler eye region; thinly clothed in whitish hairs. *Eyes*: laterals with black surrounds; fringed by whitish hairs. *Clypeus*: clothed in long whitish hairs. *Chelicerae*: pale yellow-brown with scattered fine hairs; pro- and retromargins with three teeth. *Maxillae*: pale yellow with whitish inner distal margins. *Labium*: light brownish tipped whitish yellow. *Sternum* (Fig. 12C); pale yellow-brown; shiny with scattered long pale hairs. *Coxae*: pale yellow-brown; shiny. *Abdomen*: whitish yellow mottled grey black; thinly clothed in long pale yellowish hairs; spinnerets whitish yellow suffused black. *Legs*: moderately long and slender, anterior pairs slightly more robust; generally pale yellow-brown except for legs I which have tarsi, metatarsi and tibiae lightly tinged black; spines moderately strong and numerous. Spination of legs I: metatarsi v 2-0-0; tibiae v 2-2-2; femora p 0-0-1, d 0-2-2. *Palp* whitish yellow with tarsi and tibiae suffused black. *Epigyne* (Fig. 12D–F): relatively large, thinly covered by fine hairs.

Dimensions (mm): total length 4·8; carapace length 2·04, breadth 1·52, height 1·04; abdomen length 2·88; eyes, anterior row 1·52, middle row 1·29, posterior row 1·44; quadrangle length 1·0 (49% of carapace length). *Ratios*: AM : AL : PM : PL :: 12 : 7 : 2 : 6·6; AL–PM–PL :: 8–6; AM : CL :: 12 : 2.

VARIATION. ♀ total length varies from 4·8 to 5·44 mm, carapace length 2·04–2·14 mm (four specimens).

In preserved specimens the abdominal mottling is sometimes bleached and hardly evident.

DISTRIBUTION. South Africa.

MATERIAL EXAMINED. **South Africa:** ♀ lectotype, 3♀♀ paralectotypes; Transvaal, Pretoria and Makapan, *E. Simon,* (MNHN, Paris. 20124); ♀ paralectotype, Transvaal, *E. Simon,* (MCZ, Harvard).

Cyrba lineata sp. n.

(Fig. 13A–H)

DIAGNOSIS. *C. lineata* can be recognised by the acute lobes of the caudal ledge and presence of large lateral pouches (Fig. 13G, H, arrowed).

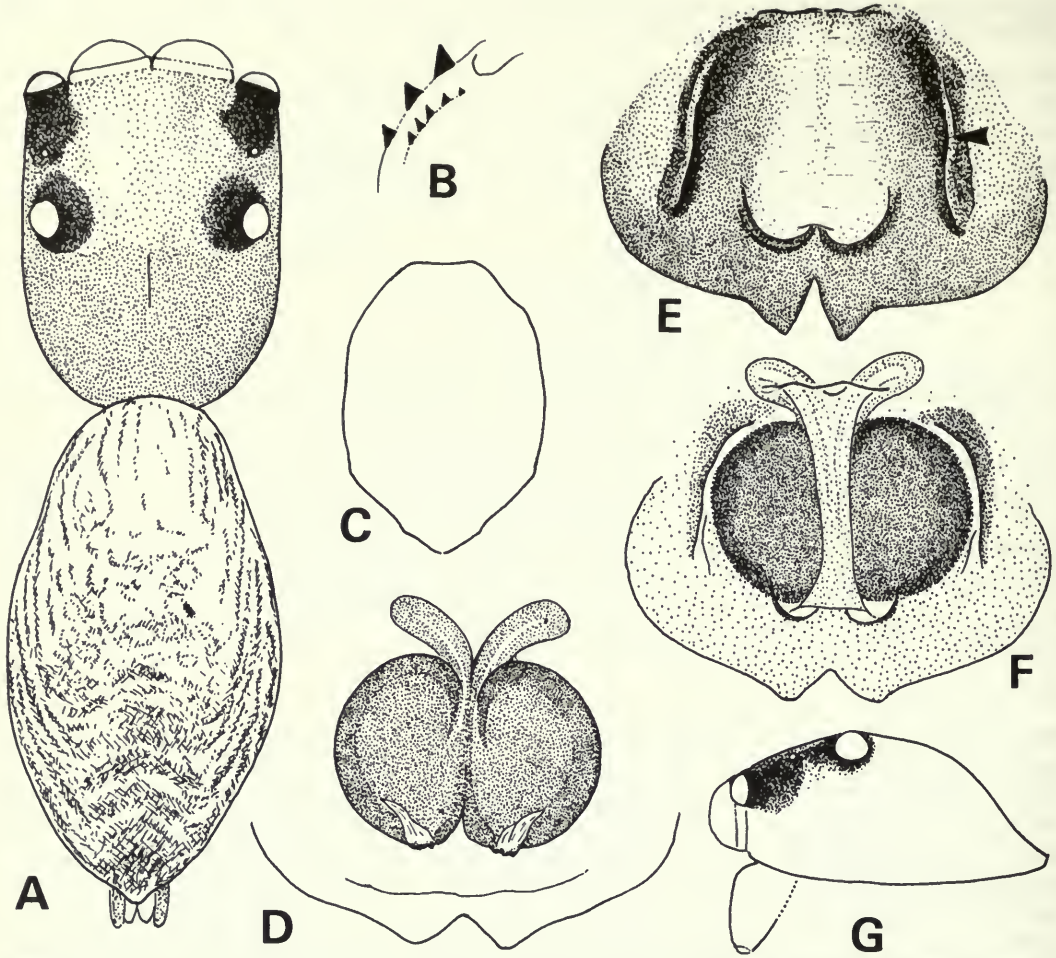

Fig. 12 *Cyrba nigrimana* Simon, lectotype ♀: A, dorsal; G, carapace, lateral. Paralectotype ♀: B, cheliceral teeth; C, sternum; D, vulva, inner view; E, epigyne; F, vulva, outer view.

MALE. Unknown.

FEMALE HOLOTYPE, in fair condition. *Carapace* (Fig. 13E): pale yellow-brown lightly tinged black in eye region; dorsum rubbed, sides clothed in greyish hairs. *Eyes*: laterals with black surrounds; fringed by pale dull amber and whitish hairs. *Clypeus*: clothed in greyish and light amber hairs, with scattered bristles and scanty marginal fringe of long whitish hairs below anterior median eyes, becoming shorter below anterior laterals and forming a scanty marginal band which extends posteriorly to about level of coxae I. *Chelicerae*: yellow-brown with sooty markings; shiny, thinly clothed in long brownish hairs; promargin with three teeth, retromargin with four. *Maxillae and labium*: pale yellow-brown with lighter tips and scattered long brownish hairs. *Sternum* (Fig. 13D) *and coxae*: pale yellow-brown faintly tinged with some black; thinly clothed in stiff blackish hairs and indistinct pale lanceolate ones. *Abdomen*: covered in short recumbent black and pale amber hairs with a thin longitudinal pale yellowish stripe and vague chevrons; venter greyish amber with brown-black hairs, bordered laterally by vague paler bands converging towards spinnerets and terminating in whitish yellow spots on either side of tracheal slit; mytiliform field greyish, fairly distinct; spinnerets yellow-brown lightly tinged black with brownish hairs. *Legs*: legs I yellow-brown suffused with some black especially on metatarsi and tibiae, clothed in greyish and black hairs with whitish ones on apices of metatarsi; other legs similar to legs I except metatarsi and tibiae paler and no darker than other segments; spines strong, most numerous on posterior legs. Spination of legs I: metatarsi v 2-0-0; tibiae v 2-2-2; femora d 0-2-2, p 0-0-1. *Palp*: femur and patella pale yellow-brown lightly suffused with some black, other segments darker and more heavily clothed in black and pale yellowish hairs. *Epigyne* (Fig. 13F): looped element of introductory ducts relatively short.

Dimensions (mm): total length c. 5·9 (pedicel stretched); carapace length 2·68, breadth 2·0, height 1·4; abdomen length 3·2; eyes, anterior row 1·96, middle row 1·76, posterior row 1·92; quadrangle length 1·28 (47% of carapace length). *Ratios*: AM : AL : PM : PL :: 15 : 8·5 : 1·5 :8·5; AL–PM–PL :: 9·5–8; AM : CL :: 15 : 3.

VARIATION. Another ♀ measures 5·9 mm total length, 2·64 mm carapace length. In this specimen (Fig. 13A) the rubbed abdomen is whitish yellow mottled black with vague chevrons

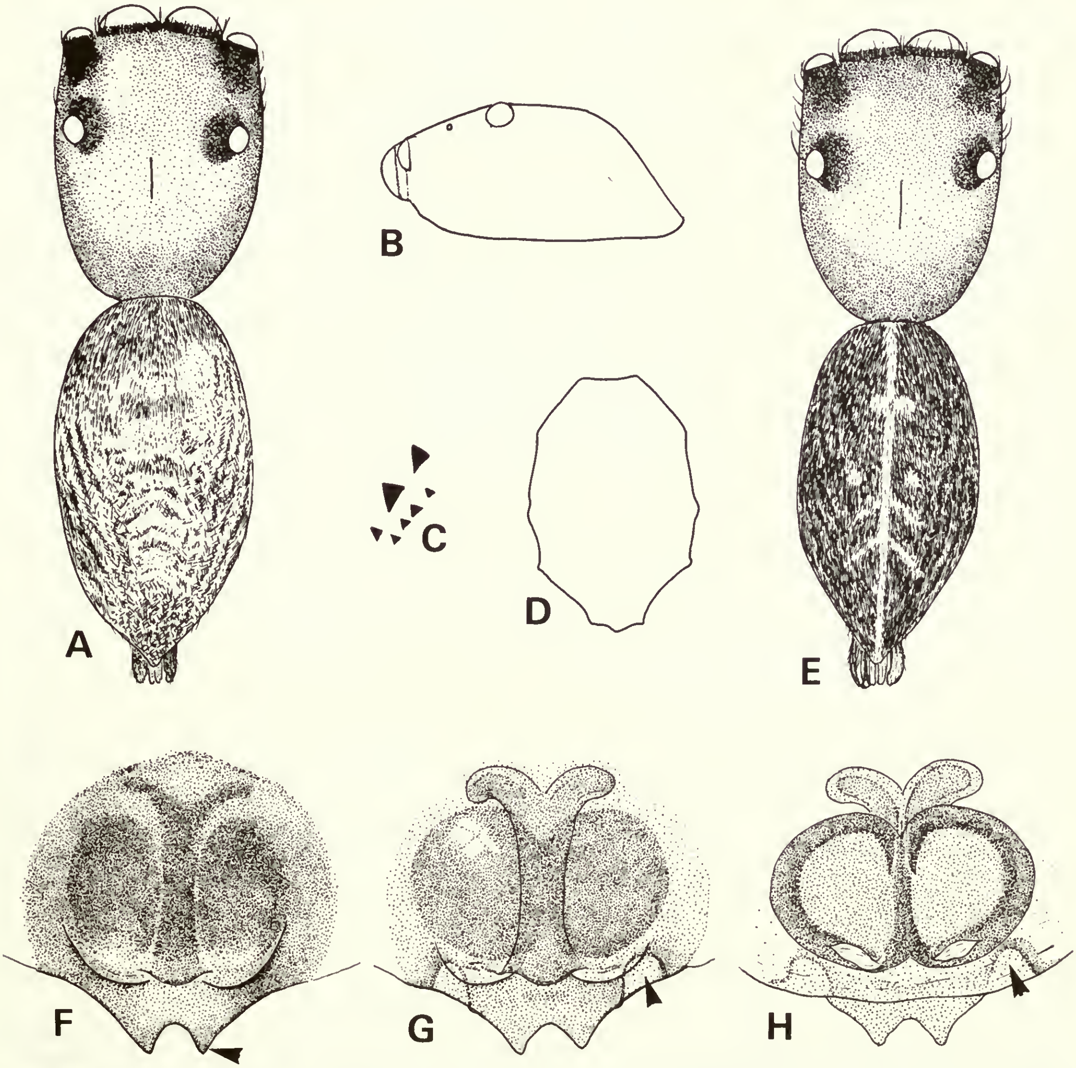

Fig. 13 *Cyrba lineata* sp. n., holotype ♀: E. dorsal; F, epigyne. Paratype ♀: A, dorsal; B, carapace, lateral; C, cheliceral teeth; D, sternum; G, vulva, outer view; H, vulva, inner view.

and scattered dark amber hairs; the dorsal stripe is not evident and the mytiliform field is obscure.

DISTRIBUTION. South Africa.

MATERIAL EXAMINED. **South Africa:** Natal, Pinetown (Durban), holotype ♀, iii.1979, *M. E. Baddeley,* (MRAC, Tervuren. 152.164); Parfuri, Kruger National Park, paratype ♀, *H. Braack,* (BMNH. 1983. 6.24.2).

Species Incertae Sedis

Cyrba armillata Peckham & Peckham

(Fig. 14A–I)

Cyrba armillata Peckham & Peckham, 1907: 606, ♀. Holotype ♀, Borneo (MCZ, Harvard) [examined]. Roewer, 1954: 985. Bonnet, 1956: 1339. Prószyński, 1971: 396.

REMARKS. The affinities of this species are uncertain, it clearly does not belong in *Cyrba* the genitalia being reminiscent of some species presently classified in euophryine groups.

FEMALE from Sarawak, in good condition. *Carapace* (Fig. 14A, C): chestnut brown with orange-brown cephalic plate and yellow-brown patch on thoracic part; clothed in shining white and scattered fine black hairs on cephalic plate with pale yellowish hairs on thoracic patch; sides largely bare except for scattered pale amber hairs. *Eyes*: with black surrounds; anteriors recurved in dorsal view, subcontiguous with apices slightly recurved in frontal; fringed by whitish and pale amber hairs. *Clypeus*: orange-brown edged by whitish hairs. *Chelicerae*: moderately robust, parallel and vertical; facies finely rugose with vague furrows; orange-brown; thinly clothed in long fine hairs; promargin with two teeth, retromargin with six. *Maxillae*: similar to ♂; orange-brown. *Labium*: similar to ♂; dark orange-brown. *Sternum* (Fig. 14D): light amber with scattered pale brown hairs. *Coxae*: yellow-brown. *Abdomen*: pale yellow-brown with sooty markings; thinly clothed in short and long greyish hairs with scattered minute shining setae. *Legs*: moderately long and slender, first pair darkest and slightly stouter; pale yellow to yellow-brown with obscure annuli on metatarsi, tibiae and apices of femora; spines numerous and moderately strong. Spination of legs I: metatarsi v 2-0-0, p 0-1-2, r 0-1-2; tibiae v 2-2-2, r 1-1-0, p 1-2-0; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Palp*: yellow-brown with fringe of grey-black hairs on inside of tarsi. *Epigyne* (Fig. 14F): copulatory openings lead into dark looped introductory ducts.

Dimensions (mm): total length 4·8; carapace length 2·08, breadth 1·76, height 1·32; abdomen length 2·48; eyes, anterior row 1·72, middle row 1·5, posterior row 1·64; quadrangle length 1·16 (55% of carapace length). *Ratios*: AM : AL : PM : PL :: 14·5 : 8 : 1·3 : 7·5; AL–PM–PL :: 9–5·5; AM : CL :: 14·5 : 5.

MALE (formerly undescribed) from Sarawak, in good condition. Habitus similar to ♀ except for the following: *Carapace*: thoracic patch less clearly defined. *Clypeus*: thinly fringed by marginal and submarginal lines of whitish hairs. *Chelicerae*: more coarsely rugose; dark orange-brown, shiny. *Maxillae and labium* (Fig. 14H): dark orange-brown. *Sternum*: orange-brown with scattered grey-black hairs. *Coxae*: first pair orange-brown, others yellow-brown. *Abdomen*: as ♀, but short black hairs lacking and pattern of sooty markings slightly more pronounced. *Legs*: legs I dark orange-brown with yellow-brown tarsi; II similar to I, but coxae yellow-brown; III and IV as II, but basal half of femora yellow-brown. Spination of legs I: metatarsi v 2-0-0, p 0-1-2, d 1-0-0, r 0-1-2; tibiae v 2-2-2, p 0-1-0, d 2-2-1, r 1-2-0; patellae p 0-1-0, r 0-1-0; femora d 0-2-4. *Palp* (Fig. 14G, I).

Dimensions (mm): total length 4·64; carapace length 2·24, breadth 1·93, height 1·48; abdomen length 2·2; eyes, anterior row 1·88, middle row 1·64, posterior row 1·76; quadrangle length 1·24 (55% of carapace length). *Ratios*: AM : AL : PM : PL :: 15 : 8·5 : 1·5 : 8; AL–PM–PL :: 10–6; AM : CL :: 15 : 5.

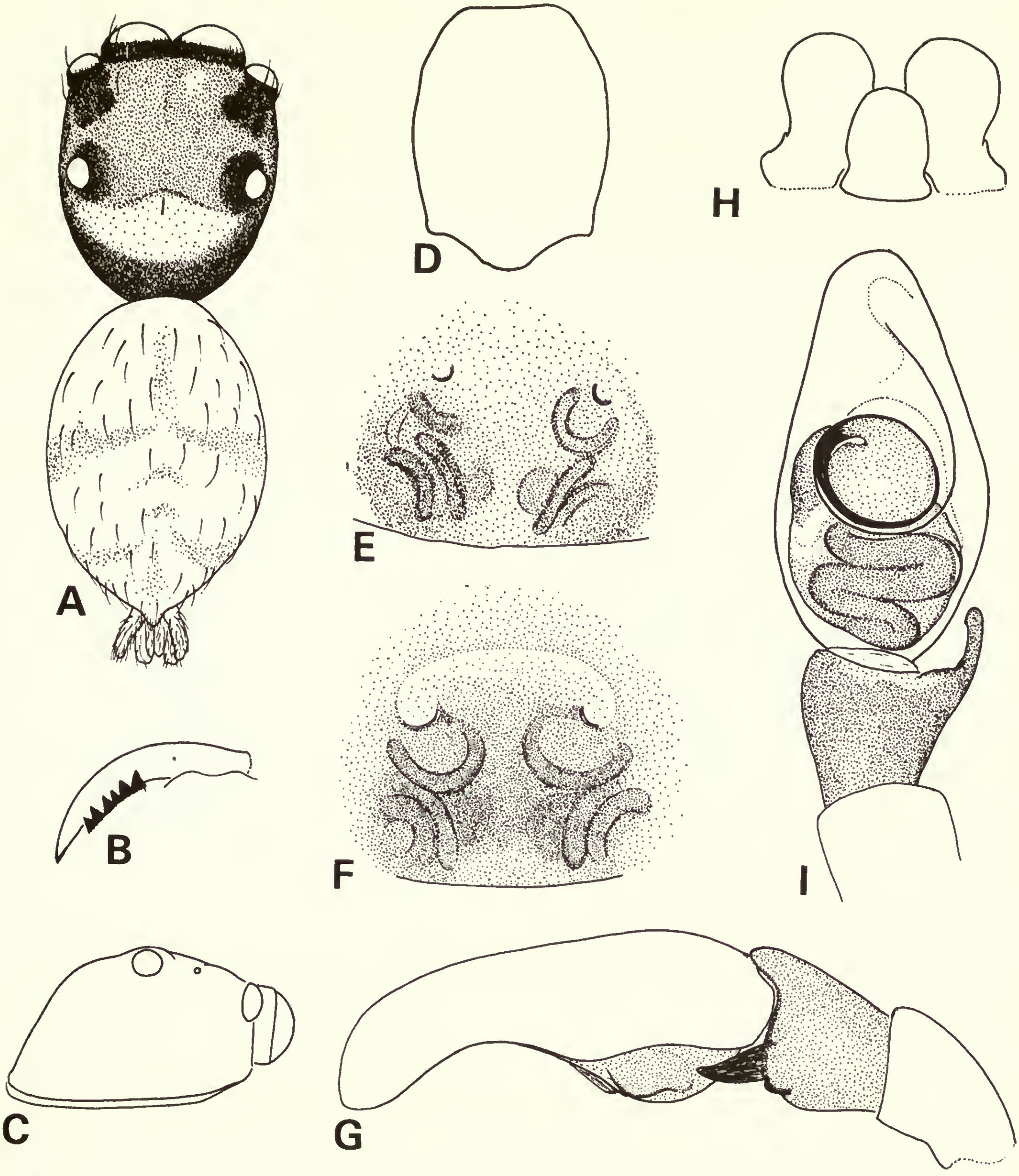

Fig. 14 *Cyrba armillata* Peckham & Peckham. ♀: A, dorsal; B, retromarginal teeth; C, carapace, lateral; D, sternum; E, epigyne of holotype; F, epigyne of Sarawak specimen. ♂: G, palp, retrolateral; H, maxillae and labium; I, palp, ventral.

VARIATION. Holotype ♀ measures c. 4·6 mm total length, 2·04 mm carapace length; epigyne (Fig. 14E).

The general habitus of the holotype and female described above are similar and the differences between the epigynes are considered to be of no significance, as they fall within the bounds of variation which might reasonably be expected to occur in this type of structure.

DISTRIBUTION. Borneo.

MATERIAL EXAMINED. **Borneo:** holotype ♀, data given in synonymy; Sarawak, Gunung Mulu National Park, on shrubs environs of base camp, 1 ♀, 1 ♂, 6.vii.1978, *F. R. Wanless*, Royal Geographical Society/Sarawak Government Expedition, (BMNH).

Cyrba dotata Peckham & Peckham

(Fig. 15A–E)

Cyrba dotata Peckham & Peckham, 1903: 185, ♀. Holotype ♀, South Africa, (MCZ, Harvard) [examined]. Roewer, 1954: 985. Bonnet, 1956: 1339. Prószyński, 1971: 396. Cutler, 1976: 131.

REMARKS. This taxon whose affinities are unknown does not belong in *Cyrba*. However, it should not be too difficult to detect related species for the presence of numerous cheliceral teeth (Fig. 15D), lack of dorsal and lateral spines on tibiae of legs I and epigynal features (Fig. 15E) are together fairly distinctive characters.

MALE. Unknown.

FEMALE HOLOTYPE, in poor condition. *Carapace* (Fig. 15A, B): dark orange-brown especially in eye region with vague blackish markings and central longitudinal yellow-brown band on thoracic part; fovea moderately long, apex just behind posterior lateral eyes. *Eyes*: with blackish surrounds; anteriors weakly recurved in dorsal view, subcontiguous with apices more or less level in frontal; sparsely fringed by whitish and long brown hairs. *Clypeus*: edged in whitish hairs. *Chelicerae*: moderately stout, slightly inclined anteriorly; dark orange-brown; fang moderately robust and evenly curved; promargin with four teeth, retromargin with eight. *Maxillae*: moderately long, more or less parallel with rounded outer distal margins; amber with inner distal margins paler. *Labium*: slightly longer than broad; pale amber tipped whitish yellow. *Coxae*: generally amber, first pair slightly darker. *Sternum* (Fig. 15C): pale amber with darker margins. *Abdomen*: detached and rubbed; yellow-brown with darker markings and paler spots (original pattern possibly distinctive); spinnerets moderately long, subequal in length; former position of colulus indicated by scanty patch of hairs between spinnerets and tracheal slit; tracheal slit indistinct, situated near base of spinnerets. *Legs*: moderately long, anterior pairs a little more robust than slender posteriors; generally amber with some black on underside of femora I and II; spines moderately strong and numerous. Spination of legs I: metatarsi v 2-0-2; tibiae v 2-2-2; femora d 0-1-3. *Epigyne* (Fig. 15E): small; the spermathecae will possibly be less distinct in fresh specimens.

Dimensions (mm): total length *c.* 6·2; carapace length 2·52, breadth 2·04, height 1·3; abdomen length 3·68; eyes, anterior row 1·8, middle row 1·64, posterior row 1·72; quadrangle length 1·16 (46% of carapace length). *Ratios*: AM : AL : PM : PL :: 14 : 8 : 1·5 : 7·5; AL–PM–PL :: 9–7·5; AM : CL :: 14 : 2.

DISTRIBUTION. South Africa.

MATERIAL EXAMINED. **South Africa:** holotype ♀, Newlands, Table Mtn. Cape peninsular, *W. F. Purcell*, (MCZ, Harvard).

Cyrba szechenyii Karsch in Lendl

Cyrba szechenyii Karsch in Lendl, 1897: 702, ♀, Hong Kong (? in TM, Budapest) [not examined]. Karsch in Lendl, 1898: 560. Roewer, 1954: 985. Bonnet, 1956: 1339.

The type of this species is believed to be in the Hungarian National Museum, Budapest, but cannot be found. Fortunately the original description is accompanied by figures, epigyne and whole animal in dorsal aspect, which show that *szechenyii* does not belong in *Cyrba*. The species will probably be rediscovered when the Hong Kong salticid fauna is well known.

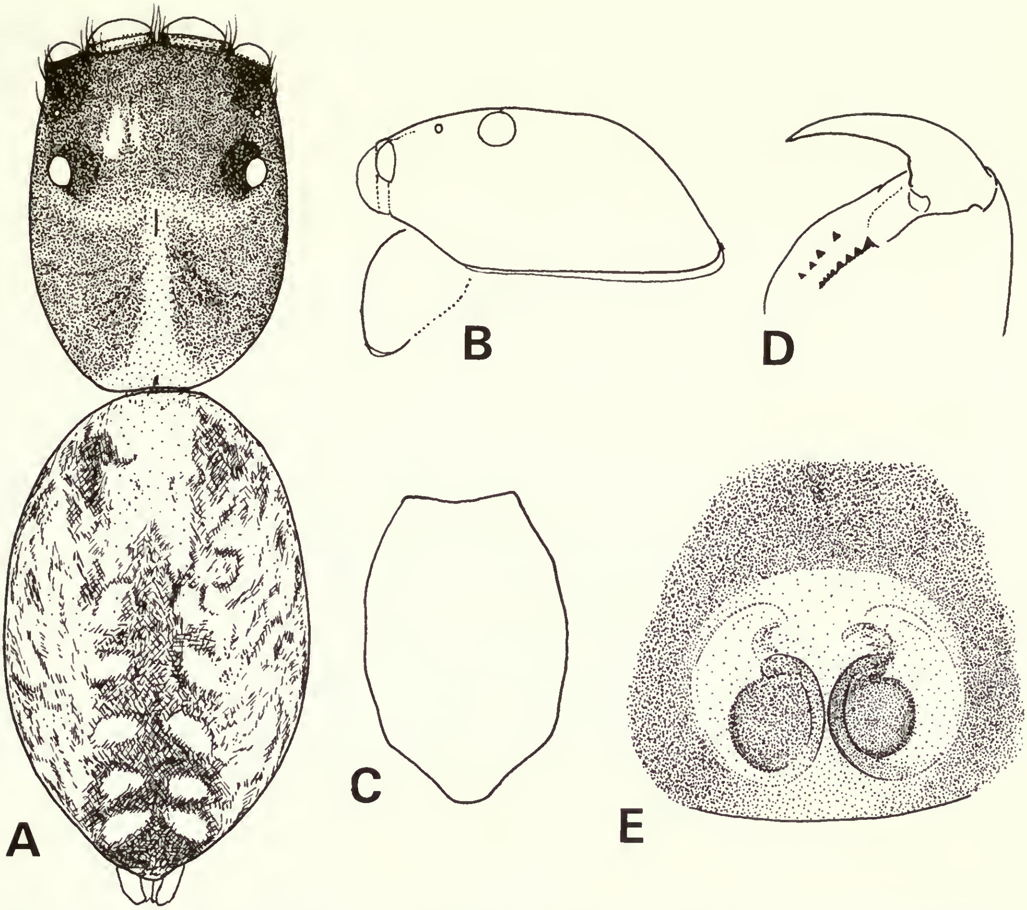

Fig. 15 *Cyrba dotata* Peckham & Peckham, holotype ♀: A, dorsal; B, carapace, lateral; C, sternum; D, chelicera; E, epigyne.

Cyrba bidentata Strand

Cyrba bidentata Strand, 1906: 662, ♀, Ethiopia, Ginir-Daua; 1909: 180. Roewer, 1954: 984. Bonnet, 1956: 1339.

The type of this species cannot be found and may have been destroyed during the 1939–45 war. To judge from the original description, especially of the epigyne, it seems to have been correctly placed in *Cyrba,* but in the absence of the type it cannot be positively identified.

Remark

Cyrba picturata Karsh in Lendl, from Hong Kong is a junior synonym of *Hasarius adansonii* (Savigny & Audouin), see Prószyński (in press).

Taxonomic summary

1. Two new species are described:
   Cyrba legendrei sp. n., and *Cyrba lineata* sp. n.

2. Three species are newly synonymised:
   Cyrba micans Simon, *Stasippus inornatus* Thorell and *Astia maculata* (Thorell) are junior synonyms of *Cyrba ocellata* (Kroneberg) itself formerly regarded as a junior synonym of *C. algerina* (Lucas).

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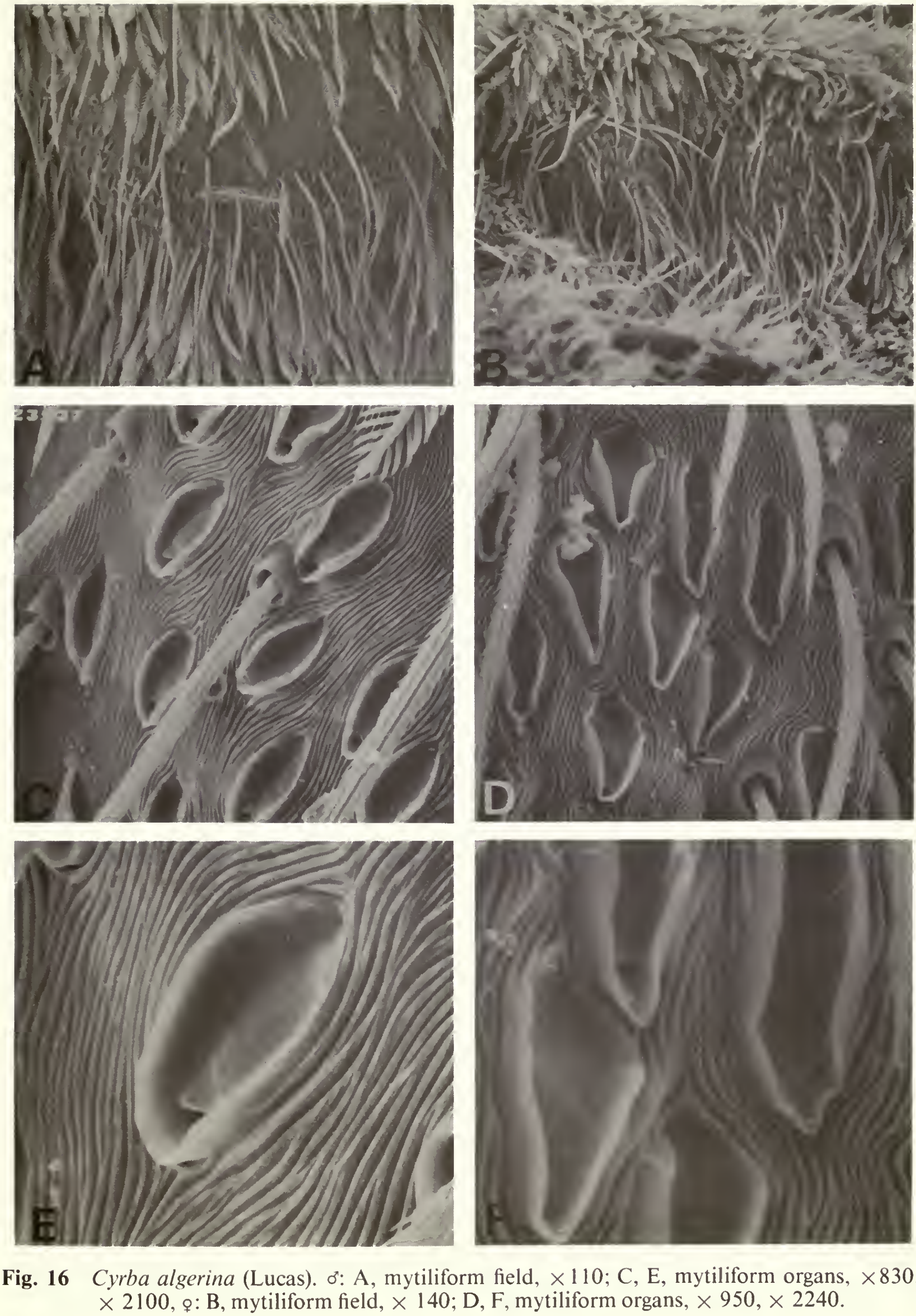

Fig. 16 *Cyrba algerina* (Lucas). ♂: A, mytiliform field, × 110; C, E, mytiliform organs, × 830, × 2100, ♀: B, mytiliform field, × 140; D, F, mytiliform organs, × 950, × 2240.

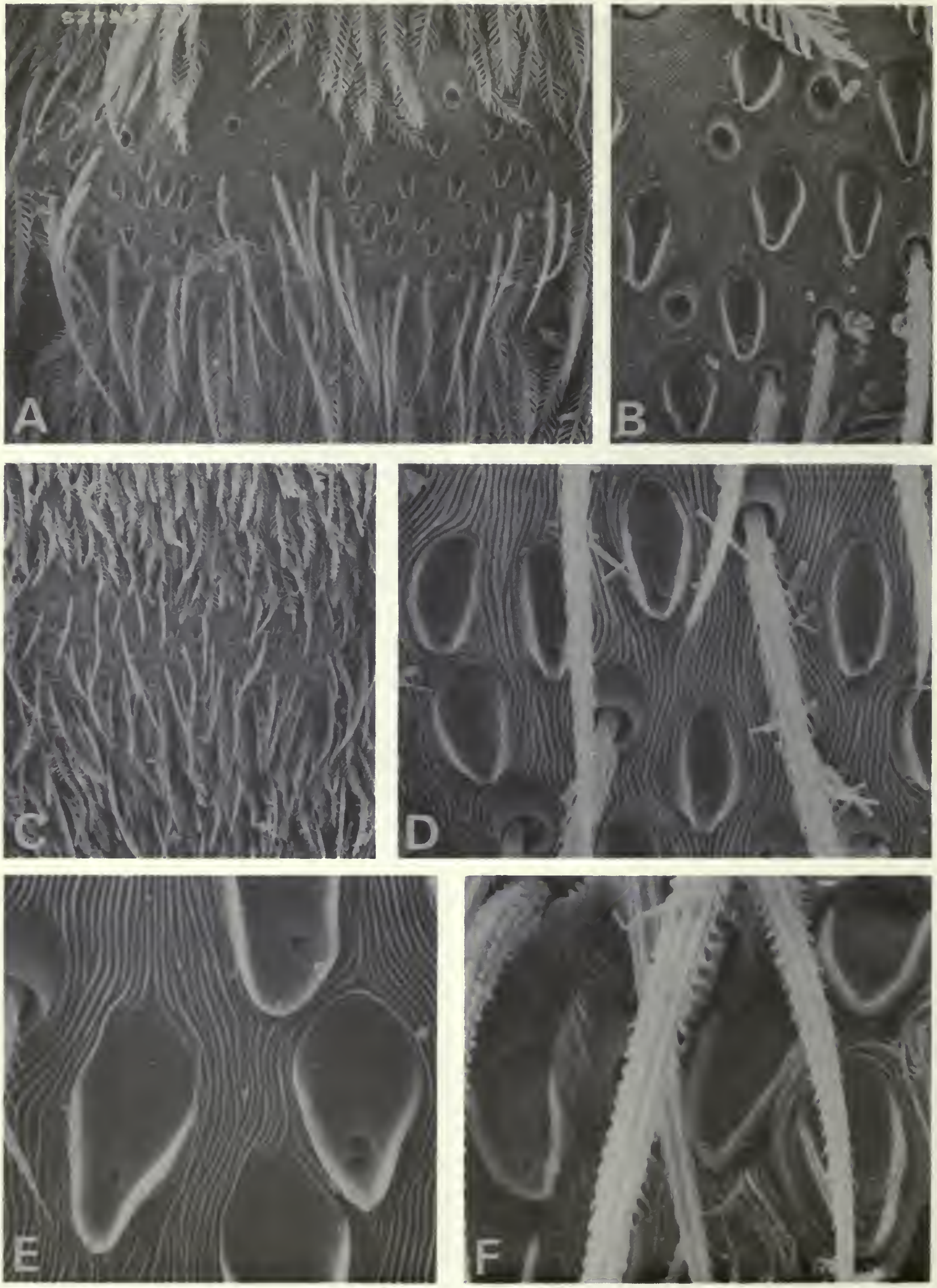

Fig. 17 (A–D) *Cyrba algerina* (Lucas). Subadult ♂: A, mytiliform field, ×230; B, mytiliform organs ×650. Subadult ♀: C, mytiliform field, ×140; D, mytiliform organs, ×1060. (E, F) *Cyrba bimaculata* Simon, E. ♂, mytiliform organs, ×1300; F, ♀, mytiliform organs, ×1500.

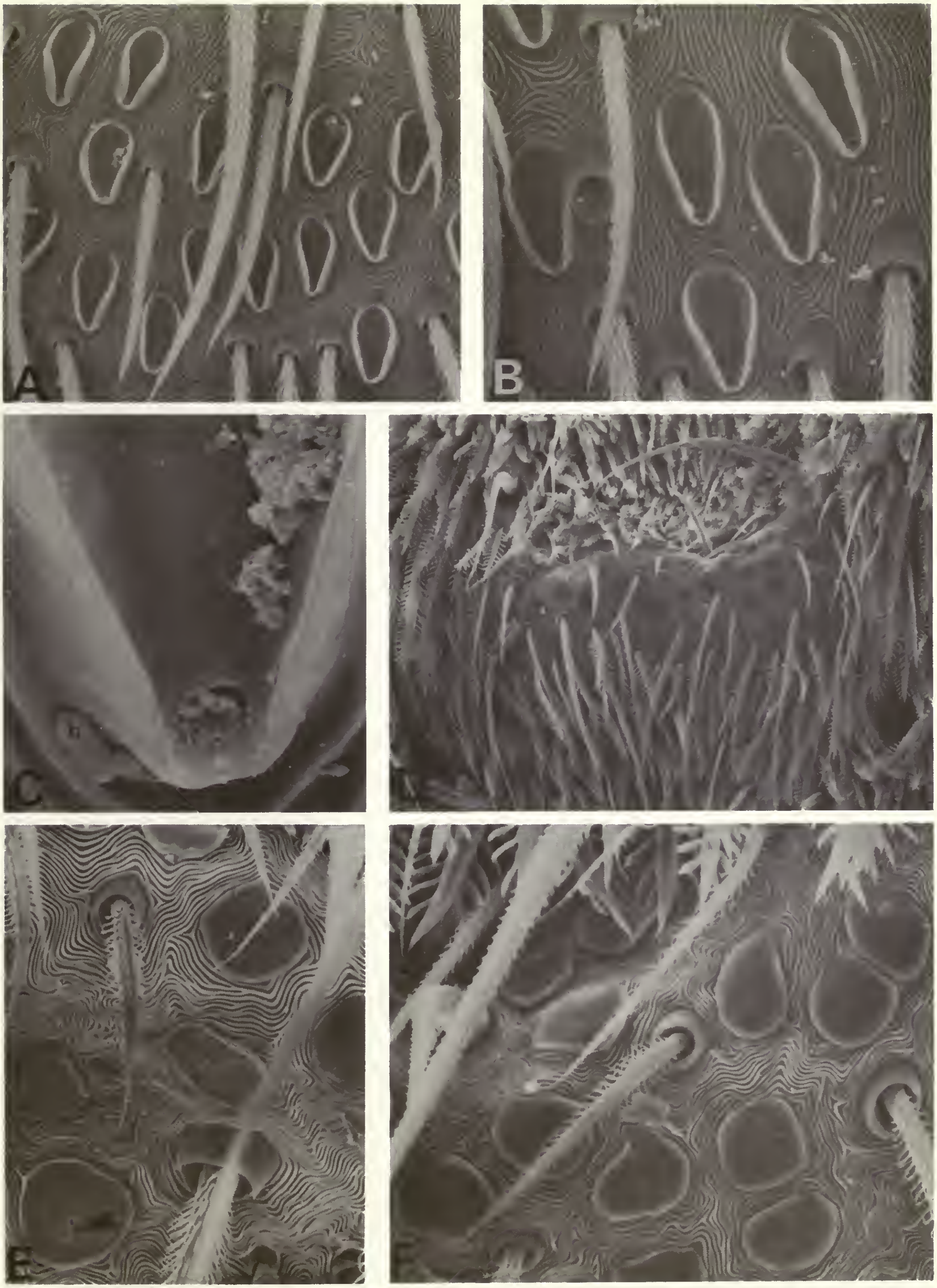

Fig. 18 (A–C) *Cyrba ocellata* Kroneberg, ♂, mytiliform organs, A, ×580; B, ×840; C, showing detritus? ×7000. (D–F) *Gelotia syringopalpis* Wanless, ♂: D, mytiliform field, ×180; E, mytiliform organs, ×1050, note sinuous gully arrowed; F, mytiliform organs ×860. Abbreviation: b, bacterium.

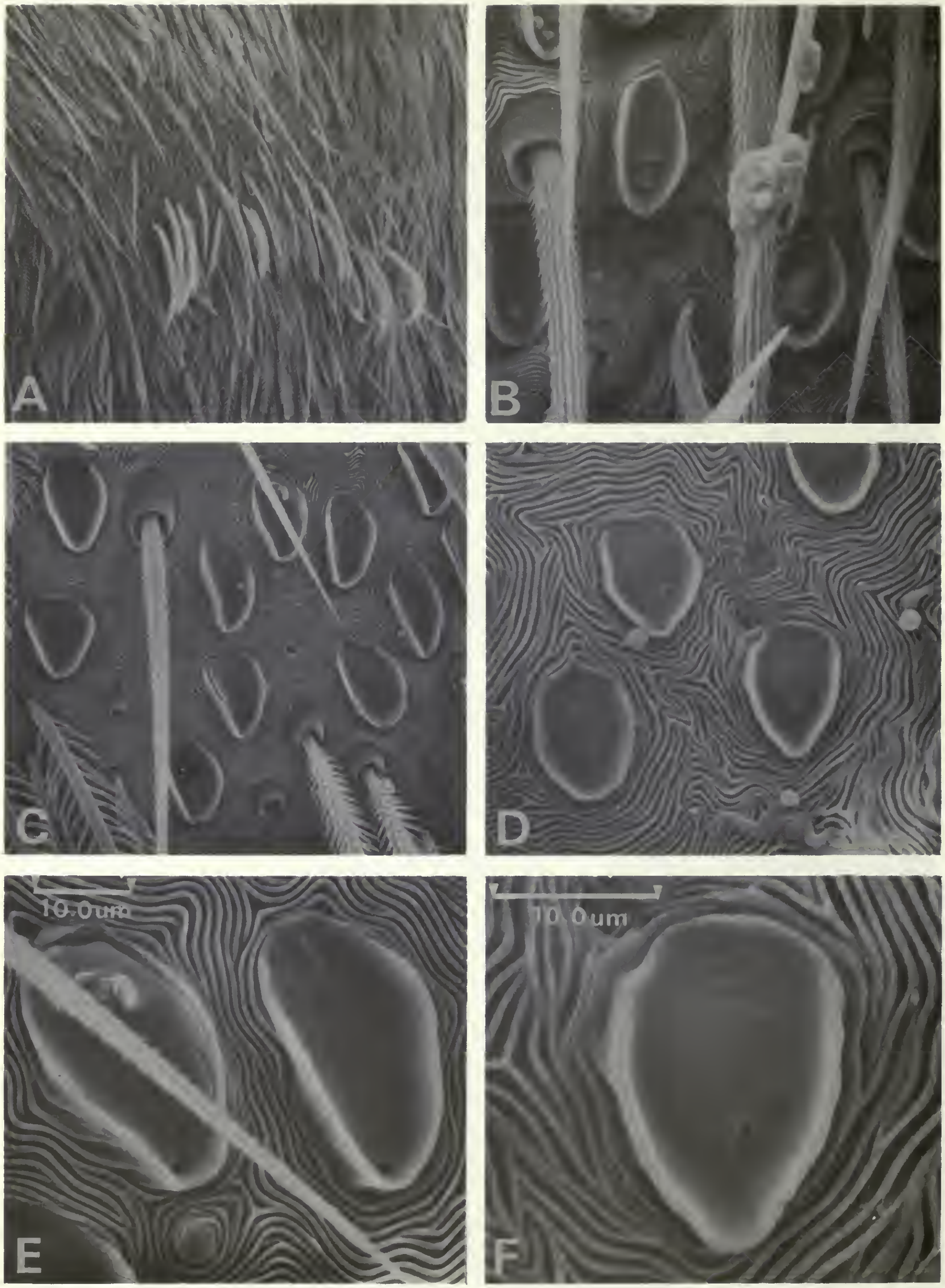

Fig. 19 (A–C, E) *Portia labiata* Thorell. ♂: A, mytiliform field, ×52; C, E, mytiliform organs, ×460, ×1400; ♀: B, mytiliform organs, ×760. (D, F) *Portia fimbriata* Doleschall, ♀, mytiliform organs, ×980; ×2400.

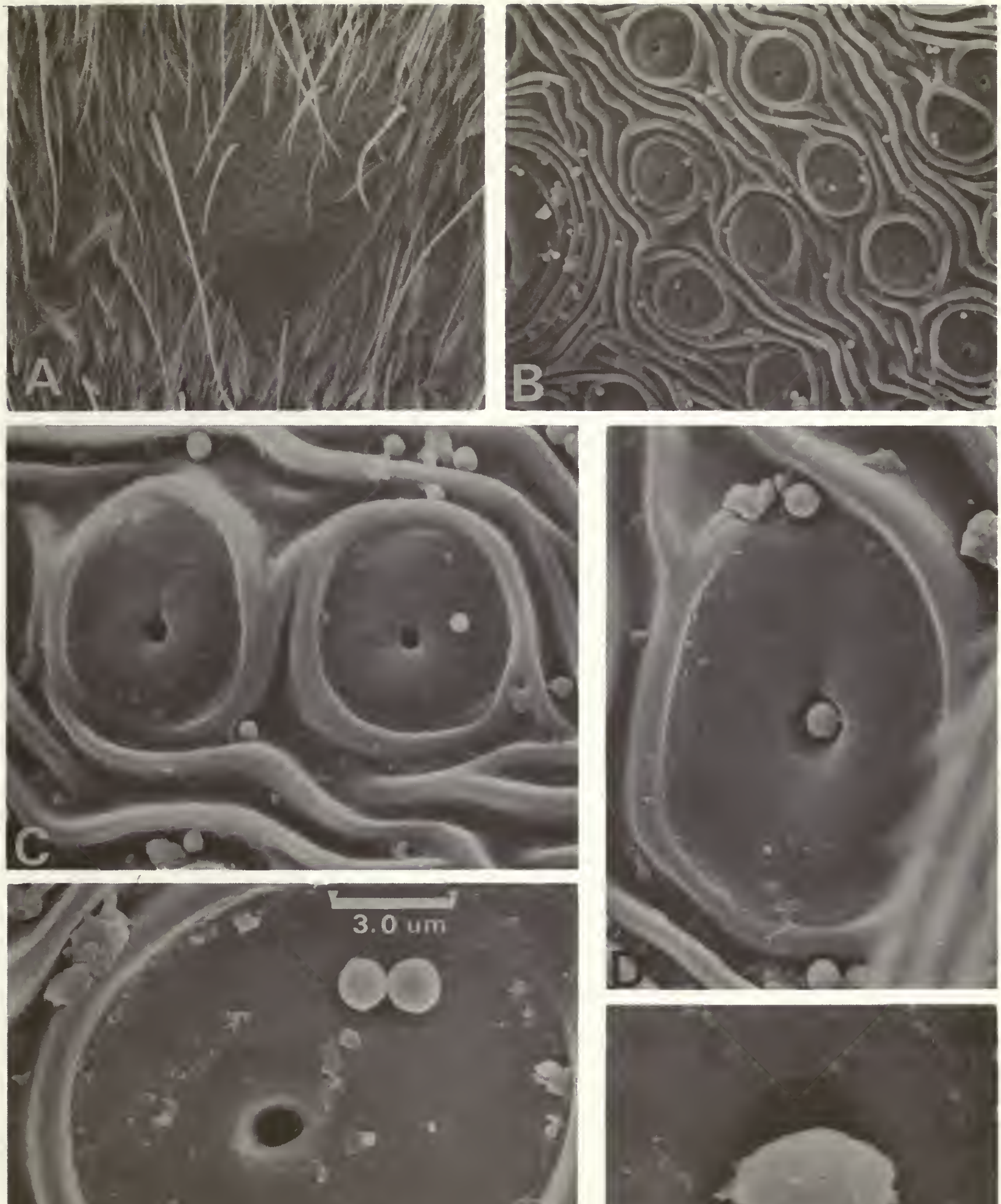

Fig. 20 (A–F) *Holcolaetis vidua* Lessert, ♀: A, pustuliform field, × 70; B–E, pustuliform organs with spheres, B, × 720; C, × 2400; D, × 3900; E, × 5500, F, distorted sphere, × 17000.

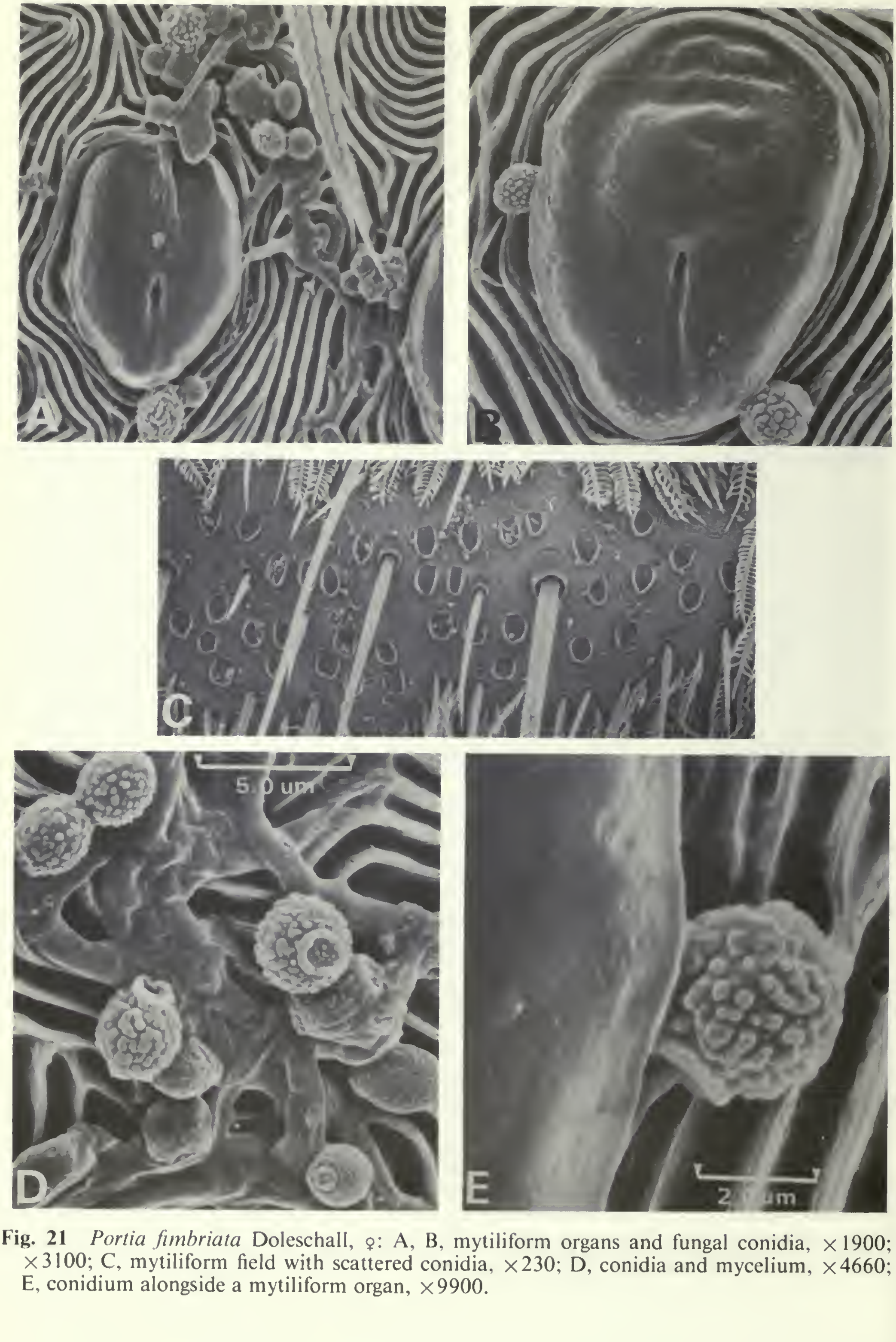

Fig. 21 *Portia fimbriata* Doleschall, ♀: A, B, mytiliform organs and fungal conidia, ×1900; ×3100; C, mytiliform field with scattered conidia, ×230; D, conidia and mycelium, ×4660; E, conidium alongside a mytiliform organ, ×9900.

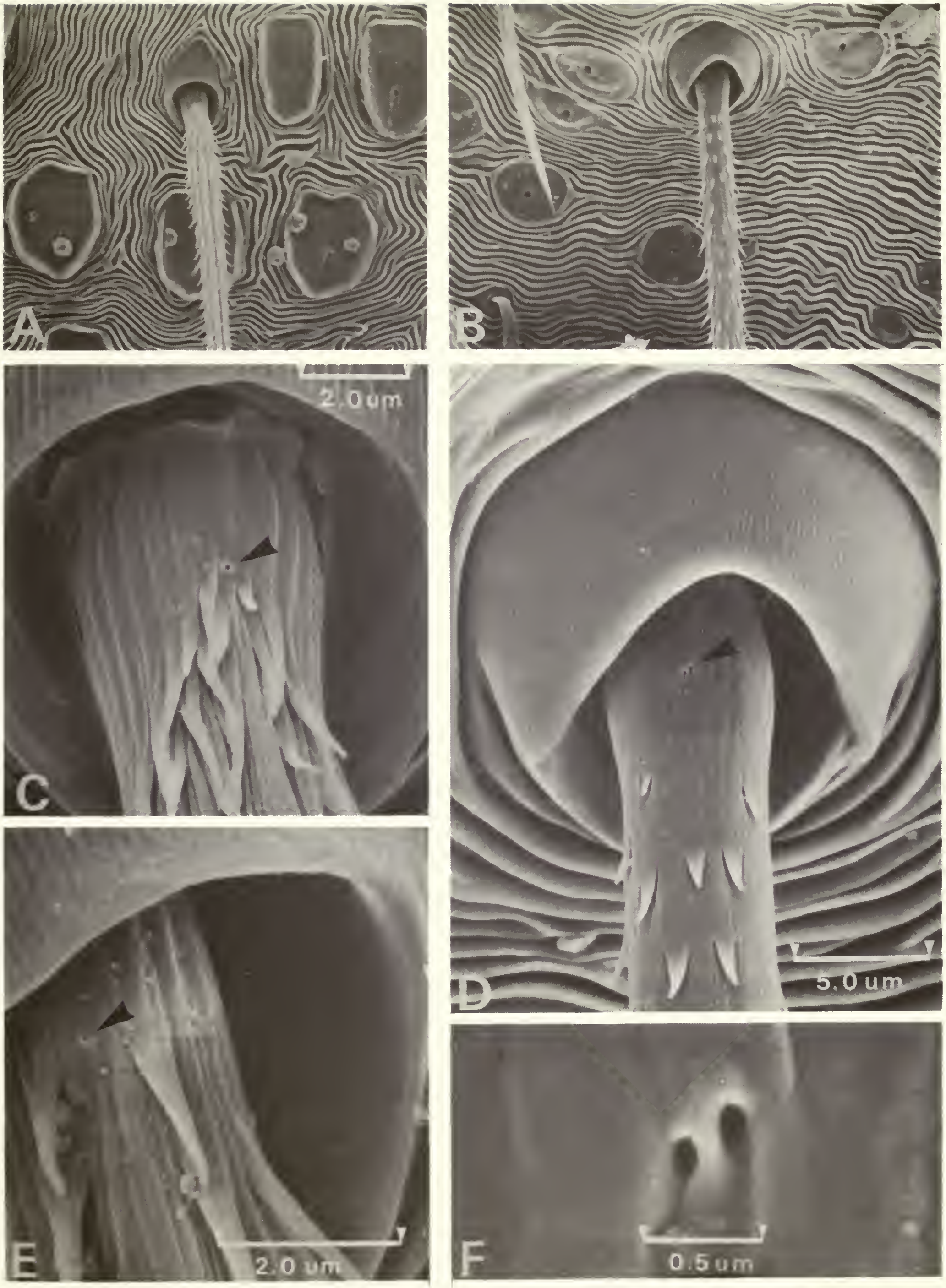

Fig. 22 (A, C) *Portia fimbriata* Doleschall, ♂: A, microseta in mytiliform field, ×880; C, base of microseta showing pore, ×7800. (B, D, F) *Holcolaetis vidua* Lessert, juvenile ♀: B, microseta in pustuliform field, ×900; D, F, base of microseta showing pores, ×4000; ×35000; E, *Cyrba bimaculata* Simon, ♂, base of microseta showing pore, ×13100.

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Dr Ethelwynn Trewavas

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